

CHAPTER 8-1

TROPICS: GENERAL ECOLOGY

JANICE M. GLIME AND S. ROBBERT GRADSTEIN

TABLE OF CONTENTS

General Ecology.....	8-1-2
Water Relations.....	8-1-5
Light.....	8-1-8
Life and Growth Forms.....	8-1-9
Nutrient Relations	8-1-12
Productivity.....	8-1-13
Climate Effects.....	8-1-16
Reproductive Biology and Phenology.....	8-1-16
Life Cycle Strategies.....	8-1-17
Mosses	8-1-18
Antheridia and Archegonia	8-1-20
Monoicous vs Dioicous.....	8-1-20
Propagules and Regrowth	8-1-21
Propagule Forms	8-1-22
Fragments	8-1-25
Spore Size	8-1-25
Diaspore Banks	8-1-25
Prolonged Protonemal Stage.....	8-1-27
Liverworts	8-1-28
Monoicous vs Dioicous.....	8-1-20
Neoteny.....	8-1-28
Reduced Numbers of Antheridia and Archegonia	8-1-29
Short Life Cycles	8-1-29
Short Spore Longevity	8-1-31
Prolonged Protonemal Stage.....	8-1-27
Types of Gemmae.....	8-1-32
Diaspore Banks	8-1-35
Rheophilic Adaptations.....	8-1-36
Dispersal.....	8-1-36
Sampling	8-1-40
Braun-Blanquet Sampling Method	8-1-40
Drying Specimens	8-1-41
Summary	8-1-41
Acknowledgments.....	8-1-42
Literature Cited	8-1-42

CHAPTER 8-1

TROPICS: GENERAL ECOLOGY

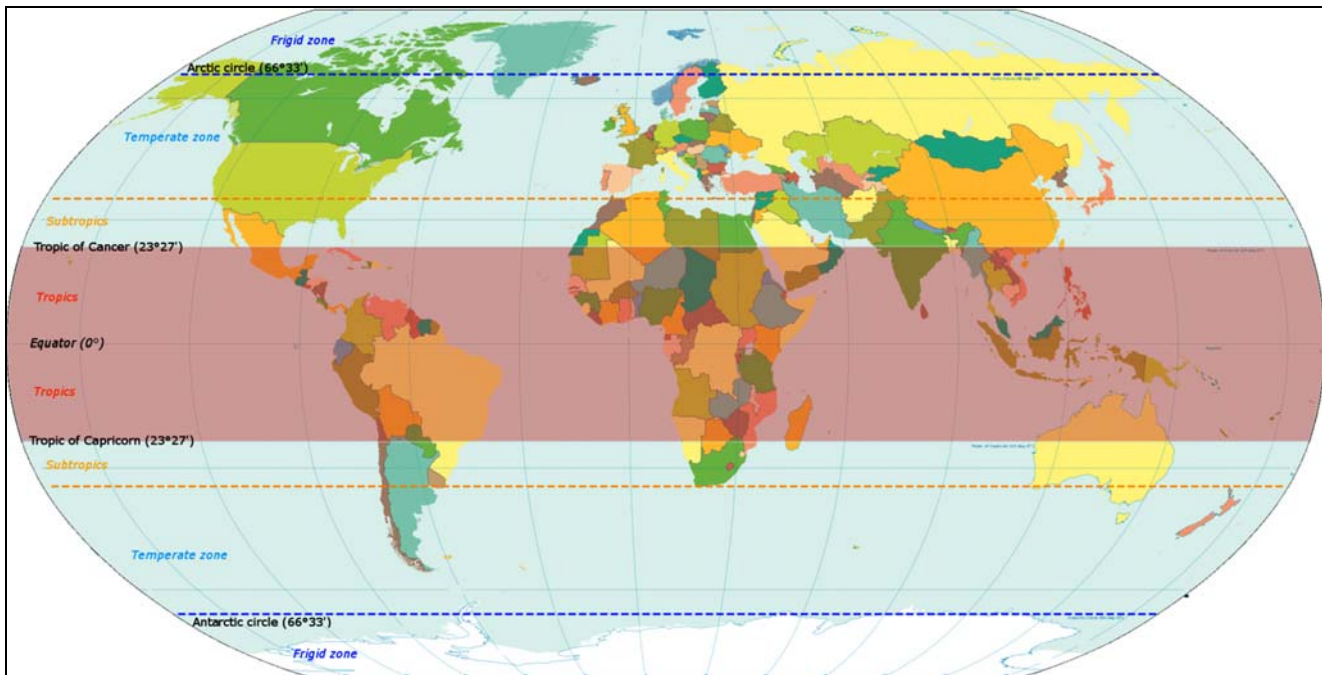


Figure 1. World map indicating tropics in pink band, subtropics in orange dotted line. Photo from KVDP, through Creative Commons.

General Ecology

Occupying the area between the Tropic of Cancer and the Tropic of Capricorn, the tropics comprise the most complex ecosystems of the world (Figure 1), extending 23°27' north and south of the Equator. The tropical land mass is nearly one-third of the land on the planet (Schuster 1988). Complex ecosystems provide multiple niches (Figure 2), and the tropics undoubtedly provide the highest number of niches anywhere with their multi-storied forests (Figure 3).



Figure 2. Tropical forest and waterfalls at Quebrada Cataguana, Honduras. Photo by Josiah Townsend, with permission.

Bryophytes in the tropics were largely ignored in early botanical studies. Resident botanists, lacking training by bryologists and preceding the development of taxonomic aids, largely ignored the bryophytes (Moreno 1992). Although bryophytes have been recorded from the tropics since the 18th century, tropical bryophyte ecology started to emerge only rather recently because keys to identify tropical bryophytes were long lacking. Early fieldwork in the tropics was done by foreign bryologists, *e.g.* Goebel (1888), Schiffner (1900), Fleischer (1904-1923) and Giesenhagen (1910) in Asia, and by Spruce (1884-1885) and Spruce and Wallace (1908) in tropical America. Spruce collected extensively in the Amazon regions and the Andes of Ecuador and Peru, and identified the liverworts himself, but gave his moss collections to William Mitten, who subsequently published them in *Musci Austro-Americani* (Mitten 1869).

Early studies on the ecology of tropical bryophytes has been summarized by Pócs (1982) and Richards (1984a). Some of the earliest studies were on **epiphyllous** (growing on leaves of other plants) bryophytes and will be discussed in the subchapter on epiphylls.

In Puerto Rico, Fulford *et al.* (1970, 1971) described liverwort communities in the elfin (cloud) forest (Figure 4). Griffin *et al.* (1974; Griffin 1979) reported on altimontane (Figure 5) bryophytes. Steere (1970) took advantage of the haploid condition of bryophytes to report on the effects of ionizing cesium radiation in Puerto Rico.

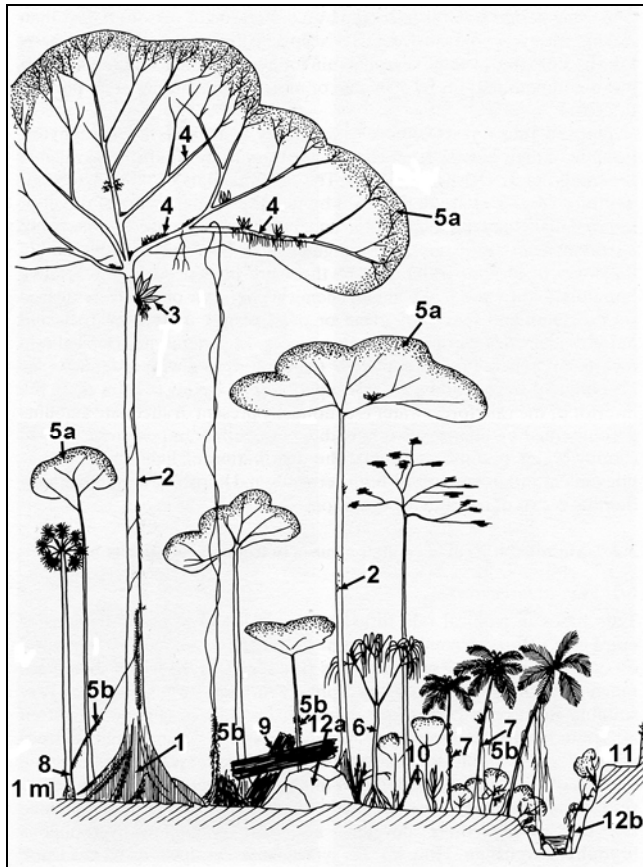


Figure 3. Microhabitats in tropical forests. **1:** Bases of large trees; **2:** upper parts of trunks; **3:** macro-epiphyte nests; **4:** bark of main branches; **5a:** terminal twigs and leaves; **5b:** bark of lianas, shrub branches, and thin trunks; **6:** *Pandanus* stems; **7:** tree fern stems; **8:** palm trunks and basal prop roots; **9:** rotting logs and decaying wood; **10:** soil surface and termite mounds; **11:** roadside banks and cuttings; **12a:** rocks and stones; **12b:** submerged or emergent rocks in streams. Image modified from Pócs 1982.



Figure 4. Elfin cloud forest fog, Luquillo Mountain, Puerto Rico, USA. Photo by Janice Glimme.

Once the bryophytes were better known, bryologists began asking ecological questions (e.g. Frahm & Gradstein 1990). Based on the results of elevational transect analyses throughout the tropics, Frahm & Gradstein (1991) recognized five tropical rainforest belts using bryophytes as indicators: lowland rainforests (Figure 6-Figure 7), submontane rainforests (=premontane rainforest; Figure 8), lower montane rainforests (Figure 9), upper montane rainforests (Figure 10), subalpine rainforests (Figure 11).



Figure 5. Drakensberg, South Africa, altimontane region. Photo by Diriye Amey, through Creative Commons.



Figure 6. Lowland rainforest tree in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.



Figure 7. Canopy in lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.



Figure 8. Submontane rainforest, Peruvian Andes. Photo by Robbert Gradstein, with permission.



Figure 9. Lower montane forest in Colombia, rich in lignified vascular epiphytes. Photo by A. M. Cleef, courtesy of Robbert Gradstein.

To further complicate our ecological understanding, early differences in methodology made ecological comparisons nearly impossible, while poor understanding of the taxonomy gave that area of study priority and limited the kinds of ecological studies that were feasible. The earliest limited ecological studies have included the relationships among climate, mountain topography, vegetation zones (Pócs 1976), ecology, reproductive biology, and dispersal trends (Schuster 1988), biomass (Frahm 1990b), water relations, and CO₂ exchange (Zotz *et al.* 1997).



Figure 10. Upper montane forest, Pui-Pui Protection Forest, Peru. Photo by E. Lehr and R. von May, through Creative Commons.



Figure 11. Subalpine dwarf mossy *Polylepis* forest in Ecuador. Photo by K. Romoleroux, courtesy of Robbert Gradstein.

Richards (1984a) provided a very useful overview of the ecology of tropical forest bryophytes, making it clear that studies at that time were limited and his coverage was superficial. One of the things that quickly becomes obvious is that most of the known ecological information relates to **epiphytes** (growing on other plants). This is because most of the tropical bryophytes are epiphytes, limited by low light levels and leaf burial on the forest floor.

In the Luquillo Mountains of Puerto Rico (Figure 12), three environmental factors cause contrasting communities of leafy liverworts (Bryant *et al.* 1973). Using area x area (**Q-mode**) analysis, they demonstrated that high-altitude liverwort communities contrast with those of low altitudes, shaded, moist habitats contrast with open, exposed habitats of all elevations, and disturbed low-elevation habitats contrast with less disturbed habitats of all elevations. **R-mode** analysis (species x species) produced nearly identical results to those of Q-mode.



Figure 12. Luquillo Mountains, Puerto Rico. Photo by Stan Shebs, through Creative Commons.

For recent species lists of tropical studies, see Gradstein *et al.* (2001) for tropical America, Churchill *et al.* (2010) on Bolivia, and many others. For additional older studies and reviews of tropical bryophyte species lists and ecology, see Delgadillo (1976) on Mexico; Lisboa (1976) on the Amazon; Egunyomi (1978) on distribution of pantropical *Octoblepharum albidum* (Figure 13) in Africa; Pócs (1982) on tropical forests; Gradstein *et al.* (1983) on Neotropical-African liverwort disjunction; Richards (1984a, b, 1988) on tropical forest ecology; Linares (1986) on the high Andes; Gradstein & Pócs (1989) on tropical rainforest bryophytes; Frahm & Gradstein (1990, 1991) on bryophytes as indicators of tropical rainforests; Frahm & Kürschner (1992) on tropical rainforests in general; Frangi & Lugo (1992) on biomass and nutrients in a Puerto Rico floodplain; Delgadillo (1993) on Neotropical-African disjunction; Miehe & Miehe (1994) on ecology in East Africa; Lösch *et al.* (1999) on Central African photosynthesis; Merwin & Nadkarni (2002) on tropical ecology, and others.



Figure 13. *Octoblepharum albidum*, a species that produces most of its juvenile, immature, and mature gametangia during the rainy season in tropical Brazil. Photo by Niels Klazenga, with permission.

Water Relations

In general, tropical adaptations reflect moisture conditions, with light and other factors being secondary (Frahm 1990a). Hence, we find that lowland forests are dominated by **mats**, and montane and cloud forests by

wefts (loosely interwoven, often ascending growth form). Thiers (1988) reported the leafy liverworts *Radula* (Figure 109), *Frullania* (Figure 14), and various *Lejeuneaceae* (Figure 128-Figure 129) to exhibit the mat growth form on their bark substrate; these taxa tend to lack dominance in the main axis. Where they form extensive mats on tree boles, they are able to trap water as it runs down the tree.



Figure 14. *Frullania* sp. from the Neotropics, demonstrating mat growth habit. Photo by Michael Lüth, with permission.

Studies on water relations seem to have been more common than other areas of tropical bryophyte ecology. Pócs (1980) studied the water interception and retention by bryophytic cover (biomass) in different types of tropical forest, forming the basis for all other studies on the subject. He found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic biomass in rainforest climates. Rainfall and epiphytes will be discussed in Chapter 8-3 of this volume.

When working on disturbance, Norris (1990) suggested four aspects of water relations that required consideration: hydration/dehydration frequency; hydration duration; dehydration duration; degree of water loss. We have since learned that rate of dehydration is important (Greenwood & Stark 2014). As Norris (1990) further surmised, these are all biomass-dependent functions, wherein large colonies typically maintain hydration longer than smaller colonies. Lateral branching of the colony allows lateral movement of capillary water. This spread of the water extends to clones that are in contact with each other. On the other hand, when tufts and cushions are separated, they contribute little to lateral spread of the water over the substrate.

Johnson and Kokila (1970) experimented with ten species of tropical mosses to determine their resistance to desiccation. These were exposed to relative humidities ranging 10-76% for four hours. After a recovery period of 24 hours, the researchers found the mosses could be divided into high and low resistance groups. Those species in the high resistance group occur in tropical forests with low humidity.

Pócs (1980) found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic bryophyte biomass in rainforest climates. As demonstrated by Larson (1981) mosses with a large surface area to weight ratio are able to absorb water very rapidly.

Thompson *et al.* (1994) calculated the bryophyte cover on a single tree of *Sloanea woollsii* (Figure 15-Figure 16) in a notophyll forest of southeast Queensland, Australia, to be 66 sq m. Water collected by the bryophytes in a single rainfall event exceeded that of the maximum daily transpirational loss from the host tree. Hence, bryophytes can contribute significantly to the relative humidity of the forest through evaporation.



Figure 15. *Sloanea woollsii*, a species known for a large cover of bryophytes. Photo by Peter Woodard, through public domain.



Figure 16. *Sloanea woollsii* forest, where many bryophytes grow. Photo by Pete the Poet, through Creative Commons.

Frey *et al.* (1990) recognized three principles of water conduction and storage by plants. In the wet season, it is

necessary to drain off surplus water. In the dry season, storage and use of condensation of water vapor are important. Above 1700 m, structures that encourage condensation from water vapor aid in water capture. They felt that leaves with grooves could permit support as well as a means of draining off excess water, an adaptation that seems to reach its maximum in the cloud forest and subalpine zone. In the lowland forest, water sacs, mats, and smooth bark combine to preserve water during short dry periods.

Karger *et al.* (2012) considered air humidity to be one of the most difficult and time-consuming climatic measurements to obtain. Thus, they tested the use of bryophyte cover as a proxy, a suggestion proposed by van Reenen and Gradstein (1983), van Reenen (1987), and Frahm and Gradstein (1991). Using 26 study sites in tropical forests, these researchers considered the possibility of using bryophyte cover as a surrogate for relative humidity as a climatic measurement. They found only a weak correlation between bryophyte cover and relative humidity across all the sites. However, when the highland (1,800-3,500 m asl) data were separated from that of the lowland (<1,800 m asl) sites, relative air humidity had a significant and distinct relationship to bryophyte cover ($R^2 = 0.36-0.62$). Temperature, on the other hand, was related to bryophyte cover only in the lowlands ($R^2 = 0.36$). The researchers concluded that epiphytic bryophyte cover can be used as a proxy for air humidity if both temperature and altitude are considered, but cover might not be a good proxy across extensive elevational gradients or wide temperature differences.

Proctor (1990) has demonstrated the reasons for bryophyte distributions through the use of physiological experiments. Whereas many bryophytes tolerate drying, even down as low as 5% water by dry weight, their photosynthesis declines rapidly as water is lost. Regaining photosynthesis can be rapid or slow upon remoistening, depending on the species and the drying conditions. In the tropics, it is important to know that most bryophytes are shade plants, even when they grow in habitats with lots of sunlight, due to their low chlorophyll *a:b* ratios. This means that they become light-saturated at relatively low light levels and do not benefit when the canopy opens up, admitting more light. But it also means that photosynthesis does not occur at a high rate, so having moist conditions provides them with a longer period of photosynthetic activity.

Both moisture and light relationships can be seen easily within a single tree as well as between habitats. For example, when Sillett and coworkers (1995) compared bryophyte diversity in a cloud forest and pasture in Costa Rica, they found 127 species of bryophytes (50 mosses, 76 liverworts, 1 hornwort) in the crowns of just 6 *Ficus tuerckheimii* (Figure 17) trees in the lower montane wet forest. Of these, 109 species were on 3 intact forest trees and only 76 on 3 isolated trees, the isolated trees having more macrolichen cover. The isolated trees were more subject to drought conditions, with higher evaporation in the inner crowns and more exposure to sunlight. The higher moisture of the intact forest supported not only a greater bryophyte species richness and cover, but also a greater frequency of **pendants, tall turfs, tails, and fans**. Furthermore, 52 species were found only on the intact

forest trees, whereas only 18 were exclusive to the three isolated trees.



Figure 17. *Ficus tuerckheimii*, a strangler fig, substrate for significant bryophyte cover in Costa Rica. Photo by Dick Culbert, through Creative Commons.

Cardosa (2012) described the hydrological cycle and the implications of climate change, using data from a La Réunion cloud forest. As already noted, the bryophytes intercept both fog and rainfall over their entire surface. This ability is important in the hydrological cycle of their ecosystems. Using two liverwort species, *Mastigophora diclados* (Figure 18-Figure 19) and *Bazzania decrescens* (see Figure 20), they determined biomass, water storage capacity, atmospheric and cloud water interception, and photosynthetic response to desiccation. Compared to *M. diclados*, *B. decrescens* stored water at approximately double the mean and maximum per hectare while at the same time occupying less than half the bryophyte volume of *M. diclados*. On the other hand, *M. diclados* had a greater ability to intercept the atmospheric moisture. Both species showed a significant relationship between photosynthesis and water content, with both species losing photosynthetic capacity at both low and high water contents. If the clouds lift, as they are predicted to do by the global climate change models, these bryophytes will most likely not survive and their role in the water cycle will be lost.



Figure 18. *Mastigophora diclados* habitat. Photo by Claudine Ah-Peng, with permission.



Figure 19. *Mastigophora diclados*, a species that stores only half the water stored by *Bazzania decrescens*. Photo by Claudine Ah-Peng, with permission.



Figure 20. *Bazzania* sp. from the Neotropics. Photo by Michael Lüth, with permission.

In addition to decreasing diversity, tropical bryophyte productivity is already being impacted by global climate change (Zotz & Bader 2008; Jácome *et al.* 2011; Song *et al.* 2012; Pardow & Lakatos 2013). Jácome and coworkers

used transplanted communities to determine potential climate change effects on the ecology of these bryophyte species.

As a result of climate change, periods of drought are becoming longer and microclimatic conditions are drier (Pardow & Lakatos 2013). Unfortunately, few physiological studies are available on tropical bryophytes, and even less is known about community responses. Pardow and Lakatos, in the first pilot study for effects of climate change on bryophyte ecology in the tropics, used chlorophyll fluorescence to indicate recovery of bryophytes from a tropical lowland forest in French Guiana (Figure 21). They found that canopy species were well adapted to desiccation events, with 13 of the 18 species maintaining more than 75% of their photosynthetic capacity after recovery from 9 days of desiccation at 43% relative humidity. Understory species were sensitive and could recover only if the relative humidity did not go below 75%. Water vapor, as one might find in fog, was sufficient to rehydrate and reactivate photosynthesis in all of these bryophytes.



Figure 21. Top of lowland rainforest canopy, French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Additional discussions of water relations as they relate to habitat can be found in the following subchapters.

Light

Although moisture is the overriding factor in bryophyte distribution in most of the tropics, light is limiting near the forest floor in well-developed multi-story rainforests (Richards 1984a; Cornelissen & ter Steege 1989). Cornelissen and ter Steege demonstrated that true sun epiphytes increase in photosynthetic rates with

increasing light intensity, even when that intensity is very high and atmospheric humidity is low. Hosokawa *et al.* (1964) found that the vertical gradient of bryophyte and other cryptogamic species and growth forms is somewhat related to light and atmospheric humidity, with the lowermost canopy species being more limited by illumination and the uppermost occurrences of trunk species being limited by insufficient atmospheric humidity.

Although high temperatures may be detrimental to some species, Barkman (1958) considered that these are probably not damaging to the bryophytes, but rather that direct solar radiation may be harmful. He cited examples of adaptive coloration exhibited by some bryophytes. Cornelissen and ter Steege (1989) found red to black pigmentation represented in many sun epiphytic species, including *Orthotrichaceae*, *Frullania* spp., and several members of holostipous *Lejeuneaceae*. The upper canopy species *Frullania apiculata* (Figure 22), *F. kunzei* (Figure 23), and *F. nodulosa* (Figure 24) are always dark red I these locations. By contrast, *F. mucronata* from zones 3 and 4 is dark olive green and *F. obcordata* (Figure 25), a generalist, is more strongly pigmented with red color in zones 5 and 6 than in zone 4. Krinsky (1968) described photochemical pathways that can be used by colored pigments that protect plants.



Figure 22. *Frullania apiculata* stem, SEM, a species that is dark red in sunny locations. Photo by Matt von Konrat, with permission.



Figure 23. *Frullania kunzei*, a species that is dark red in sunny locations. Photo by Juan Larrain, with permission.

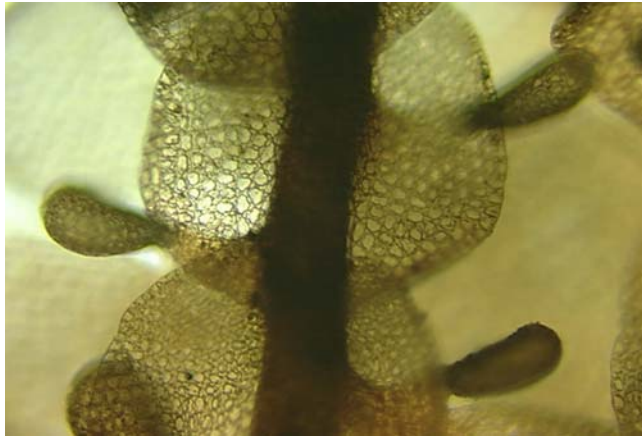


Figure 24. *Frullania nodulosa* stem ventral view, a species that is dark red in sunny locations. Photo by Matt von Konrat, with permission.

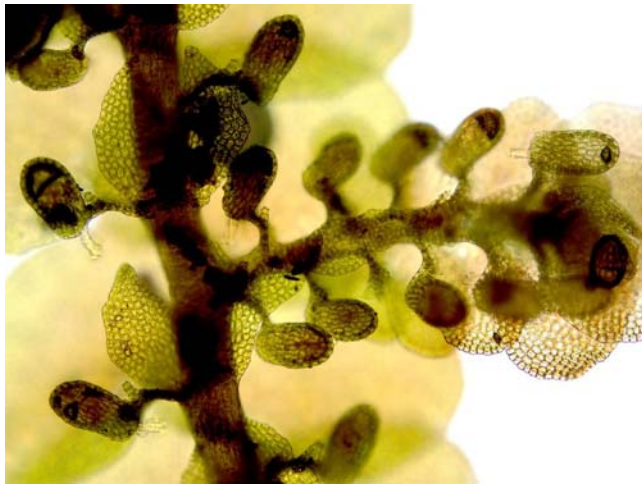


Figure 25. *Frullania obcordata*, a generalist species that is more strongly pigmented in tree zones that receive more light. Photo by Blanka Aguero, with permission.

Life and Growth Forms

Bryophyte life and growth forms reflect the habitat conditions, particularly that of available moisture. Life forms of tropical bryophytes were described in detail by Mägdefrau (1982). Aceby *et al.* (2003) found that 4-15-year-old fallows have a significantly decreased diversity of bryophyte families and mosses in Bolivia (Figure 26). Liverworts, on the other hand, have nearly as much diversity in the fallows as in the submontane rainforest. The life form is ~72% **smooth mat**, a much higher percentage than that found in the forest.

Pardow *et al.* (2012) used life forms as an indicator of high diversity in a tropical lowland cloud forest of the Guianas (Figure 27-Figure 28). These lowland cloud forests are hotspots of bryophyte diversity in tropical lowland areas compared to the common lowland rainforest, as shown in detail by Gradstein (2006) and Gehrig-Downie *et al.* (2011, 2013). The cloud forest benefits from the frequent early morning fog in the valleys. Pardow *et al.* compared the distribution of the functional groups of epiphytes across height zones in the lowland cloud forest and lowland rainforest and found a higher diversity of life forms of bryophytes in the cloud forest. In the cloud forest, **tail**, **weft**, and **pendants** are common, whereas in the

rainforest they are almost absent. The researchers suggested that identification of life forms could be used as a rapid method for identifying lowland cloud forests for conservation.



Figure 26. Bolivian old field at 600 m, surrounded by secondary forest with submontane rainforest in the background. Photo by Thorsten Krömer, courtesy of Robbert Gradstein.



Figure 27. Lowland cloud forest of French Guiana. Photo courtesy of Robbert Gradstein.



Figure 28. Canopy of lowland cloud forest in French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

In our study (Li *et al.* 1989) of *Frullania* (Figure 14, Figure 22-Figure 25) in Papua New Guinea (Figure 29), moisture and elevation gradients were important in determining taxa assemblages. Although we suspected that light and temperature were likewise important, we had no data to test these directly. Pócs (1982) and Richards (1984a, b) and a review by Thiers (1988) likewise report that the most important influences on tropical rain forest liverwort (**Jungermanniales**) growth are relative humidity, rainfall, light, and temperature (Thiers 1988). Frahm (1990a) found compensation points for two mosses in controlled temperature regimes, relating these to the tropical temperature regimes. Within this group, growth habit and stem anatomy are often modified, but perhaps the most adaptive features are the development of both simple and complex saccate leaf lobules in liverworts such as *Frullania* (Figure 22-Figure 25), presumably for retention of water, and elongate, thin-walled leaf cells.



Figure 29. Papua New Guinea. Photo from eGuide Travel, through Creative Commons.

On the other hand, excess water can be a problem because it reduces diffusion of CO₂ and can encourage fungal growth (Frey *et al.* 1990). Trees in the tropics often have leaves with prolonged (**acuminate**) tips. This has been considered by some to be an adaptation that permits water to run off the leaf, thus reducing the colonization by fungi on leaves that are subjected to daily rains. **Pendent** bryophytes in rainforests have a somewhat similar adaptation, but the interpretation has been more debatable. For example, in north temperate forests, *Frullania* (Figure 30) is recognized as a liverwort that closely adheres to its bark substrate (**mats**). However, in the rainforest, several **pendent** species of *Frullania* (Figure 31) exist (Li *et al.* 1989). One interpretation of this is again the possibility of the water to be shed by running down the rope-like plant body. However, an alternate interpretation seems to be just the opposite. The **pendent** form is actually a response to the weight of water, first in weighing down taller plants with weak stems, and then in collecting the water at the tips of the branches where the dividing cells are. Thus, the tip of the moss, during the rainy season, may be bathed in water nearly all the time, giving it a nearly aquatic environment. This continual supply of water permits the cells to divide uninterrupted by periods of drought during the rainy season. Such bryophytes can be found not only in tropical and subtropical forests such as those of southern

Japan, but also in the rainforests of the Pacific Northwest in North America.



Figure 30. *Frullania bolanderi*, an adnate species in the North Temperate Zone. Photo by Janice Glime.



Figure 31. Pendent *Frullania* from the Neotropics. Photo by Michael Lüth, with permission.

Proctor (2002) found that the **pendent** mosses *Floribundaria floribunda* (Figure 32) and *Pilotrichella ampullacea* (Figure 33) hold large amounts of external capillary water. Nevertheless, both species are able to recover from 11 months of dry storage at 5°C (not a very likely temperature in lowland tropics, but possible at some higher elevations). Both require several days to recover, with *F. floribunda* taking somewhat longer. Short desiccation periods elicit rapid recovery, with *P. ampullacea* reaching a positive carbon balance after only 30-60 minutes following 20 hours of air drying. After six days, they require 2-5 hours, suggesting that they are adapted to the short periods of desiccation found in the humid tropical forests, but not to longer, frequent periods. *Floribundaria floribunda*, on the other hand, is best adapted for more shady and continuously moist forests.



Figure 32. *Floribundaria floribunda*, a species that holds large amounts of external capillary water. Photo from Taiwan Biodiversity website, through Creative Commons.



Figure 33. *Pilotrichella ampullacea*, a species that holds large amounts of external capillary water. Photo by Jan-Peter Frahm, with permission.

In the leafy liverworts, Thiers (1988) recognized stem characters such as growth habit (projecting, prostrate, rheophytic) and anatomical characters such as epidermal thickenings, stem reduction, and stem flattening (often present in **mats**) as conserving moisture during dry periods. The flattened stems, such as those in *Pteropsiella frondiformis* (Lepidoziaceae), do most of the photosynthesizing, and accompanied by reduced leaves, the reduced life form would most likely conserve water during dry periods. Other leaf modifications include development of simple and complex saccate leaf lobules [e.g. *Pleurozia* (Figure 34-Figure 35) and *Colura* (Figure 36-Figure 37)] and presence of elongate, thin-walled, hyaline cells in the leaf margins [e.g. *Cololejeunea marginata* (Figure 38), *C. cardiocarpa* (Figure 39)], all of which help to hold or absorb water.

Further descriptions of life forms and growth forms as they relate to habitat can be found in the following subchapters. For an introduction to the topic, see Volume 1, subchapter 4-5.



Figure 34. *Pleurozia purpurea*, a species with lobules. Photo by Matt von Konrat, through public domain.



Figure 35. *Pleurozia purpurea* showing lobules with the protozoan *Blepharisma* living in them. Photo courtesy of Hess and Jan-Peter Frahm.



Figure 36. *Colura vitiensis* on leaf, Fiji Islands, a species with leaf lobules. Photo courtesy of Tamás Pócs.



Figure 37. *Colura* leaf showing lobule. Photo courtesy of Jan-Peter Frahm, with permission.



Figure 38. *Cololejeunea marginata*, a leafy liverwort species with thin-walled hyaline cells on the leaf margins. Photo by Jan-Peter Frahm, with permission.



Figure 39. *Cololejeunea cardiocarpa*, a leafy liverwort species with thin-walled hyaline cells on the leaf margins; it also has lobules. Photo by Blanka Aguero, with permission.

Nutrient Relations

Nutrients are also affected by the rainy and dry seasons. Nutrient pulses occur as bryophytes dry and rewet. Damaged membranes leak nutrients and other substances such as sugars and polyols. Rainfall leaches these nutrients from the bryophytes, including their surfaces, and carries them to the forest floor (Lodge *et al.*). These pulses synchronize nutrient availability that maintains higher rates of nutrient mineralization, plant uptake, and forest productivity. It provides nutrients at the beginning of the growing seasons, a time at which they should be most beneficial to forest species. Thus the bryophytes serve as storage units that provide nutrients at the most critical time.

Coxson and coworkers (Coxson 1991; Coxson *et al.* 1992) noted the importance of wetting/drying cycles for the accumulation of sugars and polyols to more than 950 kg ha⁻¹ in the epiphytic bryophytes of the cloud forest canopy of Guadeloupe (French West Indies). These sugars can stimulate the growth of microbes and thus facilitate the breakdown of litter. These relationships suggest some of the importances of these wet to dry changes in nutrient release from the epiphytic bryophytes (and for some, probably ground-dwelling species as well) and their role in the forest dynamics.

Further support for these responses comes from differences between upper and lower canopy bryophytes. Coxson and coworkers (1992) found that the upper canopy leafy liverwort *Frullania atrata* (Figure 40) holds 17% of its dry weight as sugar and polyol reserves. [Note that the name *F. atrata* has been misapplied to a number of tropical *Frullania* specimens, so information regarding the species may actually belong to one of its look-alikes (pers. comm. Robert Gradstein).] By contrast the lower canopy moss *Phyllogonium fulgens* (Figure 41) holds these reserves as less than 6% of its dry weight. The upper canopy bryophytes seem better adapted at retaining these, with *F. atrata* releasing only 0.3 g m⁻² compared to 0.9 g m⁻² for *P. fulgens*. This relationship was supported by similar relationships of bryophytes under field conditions in the tropical montane cloud forest of Guadeloupe, French West Indies.

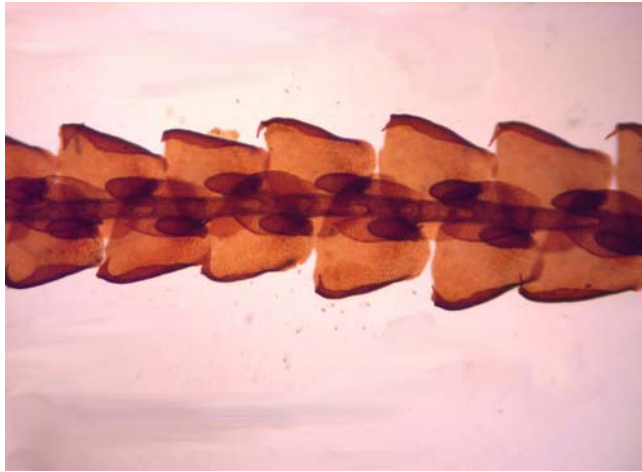


Figure 40. *Frullania atrata*, an upper canopy liverwort and a species that can hold 17% of its dry weight as sugar and polyol reserves. Photo by Juan Larrain, with permission.



Figure 41. *Phyllogonium fulgens*, a lower canopy moss in the Neotropics, where it holds less than 6% of its dry weight as sugar and polyol reserves. Photo by Michael Lüth, with permission.

Frangi and Lugo (1992) studied the biomass and nutrient accumulation in ten-year-old communities in a flood plain at the Luquillo Experimental Forest, Puerto Rico. They found a higher bryophyte cover on streambanks where flooding was frequent but of short duration. The cover decreased toward the longer-lasting flood plain, with the minimum cover occurring in depressions where water remained and became stagnant. They measured nutrient accumulations in ash-free biomass of bryophytes. These accumulations in kg ha^{-1} were 14.5 for N, 0.8 for P, 5.3 for K, 2.7 for Ca, 2.7 for Mg, 0.5 for Mn, 18.5 for Fe, and 22 for Al. These numbers were similar to those found in fine litter. Nevertheless, these values were low compared to that of other bryophyte communities. Both biomass and nutrients were greater in streambank slope communities and slopes of tree mounds than that in depressions that remained wet for a long time.

The bryophytes in these tropical flood plain communities appear to retain nutrients and serve as filters during flooding in these communities.

In the coastal forests of Kenya, some bryophytes specialize on acid or alkaline substrates (Wilding *et al.* 2016). For example, *Tortella tortuosa* (Figure 42) is strongly associated with calcareous substrates, whereas *Racomitrium lanuginosum* (Figure 43) only occurs on acid ground. These preferences most likely relate to their ability to obtain their needed nutrients, without getting them in excess.



Figure 42. *Tortella tortuosa*, a species of calcareous substrates. Photo by Michael Lüth, with permission.



Figure 43. *Racomitrium lanuginosum*, a species of acid substrates. Photo by Janice Glime.

Further discussion of nutrient relations of tropical bryophytes is in the subchapters on Epiphytes.

Productivity

Productivity studies, in particular, are difficult to compare because of differences in methodology. Moreover, few exist.

Pócs (1987) was among the early productivity researchers, examining the changes in biomass among bryophytes in the East African rainforests. As we might expect from temperate studies (Proctor 1982), physiological and experimental studies indicate that net productivity drops rapidly as temperatures rise above 25°C (Frahm 1990b). Add low light levels to the high temperatures and the bryophytes are hindered by high

respiration rates and low photosynthetic rates, resulting in low or negative net assimilation. Due to differences in precipitation, humidity, temperature, and desiccation (Frahm 1990a, b), it is generally true that biomass of epiphytic bryophytes in equatorial latitudes increases from the tropical lowlands to the treeline. Thus, high temperatures, combined with low light intensities, can account for the low diversity of bryophytes in the lowlands. Richards (1952) found data indicating that during the wet, and thus cloudy, season, the maximum temperatures in the ground layer are lower than those in the dry season when the sun shines a greater proportion of the time.

This raises the question of how the limited numbers of species in the lowlands survive. Frahm (1990b) suggested this could involve a specialized phytochrome system or more effective storage of the photosynthetic products. Perhaps more realistically, the relatively high nutrient supply that arrives through abundant precipitation could support a positive net photosynthesis. Another factor that could contribute is that the forest floor can have high CO₂ concentrations due to enhanced decomposition of leaves in a hot, moist environment, but increased CO₂ levels are most beneficial in high light levels.

Zotz *et al.* (1997) provided further information on the CO₂ and water relations for net photosynthesis. Using six tropical bryophytes, these researchers measured the daily changes in water status and net CO₂ exchange in a submontane tropical rainforest in Panama (Figure 44). Daily variation of water content was "pronounced." Both high and low water content limited carbon gain. Low light during rainstorms was less important in limiting CO₂ exchange compared to water content. More than half the carbon gain was lost at night to respiration.



Figure 44. Panamanian submontane and montane forests. Photo by S. B. Matherson, through Creative Commons.

In a more recent publication, Chen *et al.* (2016) examined photosynthetic properties of epiphytes in Southwest China. These adaptations include higher total chlorophyll concentrations, specific leaf area, and chlorophyll per unit leaf N (Chl/N), lower ratio of chlorophyll *a:b*, and greater photosynthetic nitrogen-use efficiency. Measurements, in $\mu\text{mol m}^{-2} \text{s}^{-1}$, showed means for light-saturated net photosynthetic rate (0.55), light saturation point (106.72), light compensation point (4.17) and dark respiration rate (0.25). They demonstrated

photosynthetic down-regulation under high light conditions for these low-light epiphytes. These trunk-dwelling epiphytes are adapted for high resource retention rather than high resource gain. This is accomplished by low respiration rates and low light compensation points in shady habitats.

Waite and Sack (2010) hypothesized that leaf trait values would "reflect the distinctive growth form and slow growth of mosses, but also that trait correlations would be analogous to those of tracheophytes." Using ten species from Hawaii (Figure 45), they quantified 35 physiological and morphological traits of cell, leaf, and canopy level of bryophytes growing on the ground, trunk, and canopy. These bryophytes had low leaf mass per area (A_{mass}) and low gas exchange rates. Perhaps not surprisingly, but in contrast to that of tracheophytes, the moss light-saturated photosynthetic rate per mass did not correlate with habitat irradiance. However, leaf area, cell size, cell wall thickness, and moss canopy density all correlated with microhabitat irradiance. Waite and Sack furthermore found that costa size, canopy height, and A_{mass} were coordinated traits linked with structural allocation.



Figure 45. Hawaiian forest near Hanalei Bay, Kauai. Photo by Lukas, through Creative Commons.

Wagner *et al.* (2014) sought to explain the distribution of tropical bryophytes based on their physiological ecology. They noted the increase in bryophyte biomass with altitude in rain and cloud forests. They suggested that the low bryophyte abundance in the lowland rainforests is a result of the limitation of net carbon gain during fast drying and low light levels during daytime, coupled with the moist, warm nights. These moist, warm nights promote respiration and the daytime photosynthesis can be insufficient to balance the nighttime CO₂ loss. Wagner and coworkers concluded that the timing of hydration is crucial for net photosynthetic gain.

Datta Munshi (1974) studied seasonal changes in standing crop (chlorophyll) and annual net production of two moss communities at Varanasi, India. The mean bryomass in a perennial *Hydrogonium* (Figure 46) community was 95 g m⁻² and in the seasonal community of *Physcomitrium* (Figure 47) it was only 11 g m⁻². These values represent the first on non-epiphytic bryophytes in the tropics and were lower than those typical of bryophytes in temperate forests, being more like those in Arctic ecosystems.



Figure 46. *Hydrogonium ehrenbergii*, member of a perennial genus in the Indian tropics. Photo by Jan-Peter Frahm, with permission.



Figure 47. *Physcomitrium eurystomum* capsules; this genus is a member of seasonal community in the Indian tropics. Photo by Dick Haaksma, with permission.

Tropical forests generally have a larger biomass of epiphytic bryophytes than do temperate forests (Norris 1990). However, when trees are widely spaced or occur as lone trees, the greater penetration of wind can quickly desiccate the adhering bryophytes.

Overall, bryophytes comprised 40% of the epiphytic biomass in a Neotropical lower montane cloud forest at ca. 1600 m in Costa Rica (Nadkarni 1984) compared to 6% in the leeward rainforest (Ingram & Nadkarni 1993). In both forests, bryophytes were most abundant among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dyer 1980).

In an upper montane cloud forest at 3700 m in the Andes of Colombia (near the forest line), the bryophyte contribution to total epiphyte biomass was much higher, almost 70% (Hofstede *et al.* 1993) and total epiphytic biomass (including suspended soil) was a staggering 44 tons per hectare, the highest value ever reported.

Light is an important limiting factor for photosynthesis in the tropics. For three species of *Pogonatum*, chlorophyll content and chloroplast size differed with light intensities

where they predominated (Nasrulhaq-Boyce *et al.* 2011). For *P. cirratum* subsp. *macrophyllum* (Figure 48) and *P. subtortile*, the total chlorophyll and beta-carotene content are higher than that in *P. neesii* (Figure 49). The latter lives in the areas with much higher light intensities ($751 \pm 45 \text{ W m}^{-2}$), compared to 28 ± 4 and $230 \pm 39 \text{ W m}^{-2}$, respectively. The sun species, *P. neesii*, had a higher soluble protein content, likewise having a higher soluble protein to total chlorophyll ratio. *Pogonatum cirratum* subsp. *macrophyllum*, the species from the lowest light, had significantly larger chloroplasts as well as more grana and thylakoids per chloroplast than did the other two species. And the two species from the lowest light had more than double the numbers of starch grains. On the other hand, the leaf **lamellae** (vertical stack of cells on leaf; Figure 50) were shortest in the species receiving the lowest light levels. Nevertheless, the CO_2 assimilation rates were highest in *P. neesii* even when light intensities were low. Lamellae can provide more surface area for photosynthesis and capillary spaces to hold water longer. In low-light *P. cirratum* subsp. *macrophyllum*, these are rudimentary, whereas those of *P. subtortile* are 5-7 cells high.



Figure 48. *Pogonatum cirratum*, a species of low light and large chlorophyll. Photo by Li Zhang, with permission.



Figure 49. *Pogonatum neesii*, a species of higher light intensity and less chlorophyll than that in *P. cirratum* subsp. *macrophyllum*. Photo by Yang Jia-dong, through Creative Commons.



Figure 50. *Pogonatum* leaf cs showing leaf lamellae at two different magnifications. Photo by Michael Lüth, with permission.

Further discussions of productivity and biomass will be provided in the succeeding subchapters as they pertain to particular habitats.

Climate Effects

As noted above, moisture and temperature are important determinants of the types of bryophyte vegetation that survive. And precipitation events and cloud cover will diminish the light intensity. Among the early studies on the effects of these climate parameters on tropical bryophytes is a study by Biebel (1964, 1967). He examined temperature resistance of jungle mosses. Weber (1985) examined the effects of El Niño on bryophytes of the Galápagos. Furthermore, hurricanes can be devastating to epiphytes, ripping them from the trees or breaking branches and even toppling trees.

Rainy "seasons" are common in the tropics, punctuated by dry periods. If there are two periods in the year when the sun is overhead in the tropics, two wet seasons will occur (Richards 1952). If the two periods of overhead sun are close together, the two wet seasons will merge, but two maxima will still occur.

In the winters of many parts of the tropics, a dry season turns the area into near desert conditions. Akande (1984, 1985) attempted to understand the desiccation tolerance, or lack of it, among several tropical African bryophytes. Using the leafy liverwort *Mastigolejeunea florea* (now called *Spruceanthus floreus* according to Robert Gradstein; see Figure 51) and the mosses *Calymperes palisotii* (Figure 52) and *Entodontopsis nitens*, he concluded that these mosses were more desiccation-tolerant than the liverwort. It is interesting that bryophytes maintained at 0% relative humidity for one week and one month at 28°C were able to resume respiration more quickly than those kept at 32 and 54% relative humidity. He considered this ability to recover from 0% humidity so easily to be a case of **anhydrobiosis** (living state without water).



Figure 51. *Spruceanthus planiusculus* in a genus where some of the tropical African species are less desiccation tolerant than mosses. Photo by Claudine Ah-Peng, courtesy of Robert Gradstein.

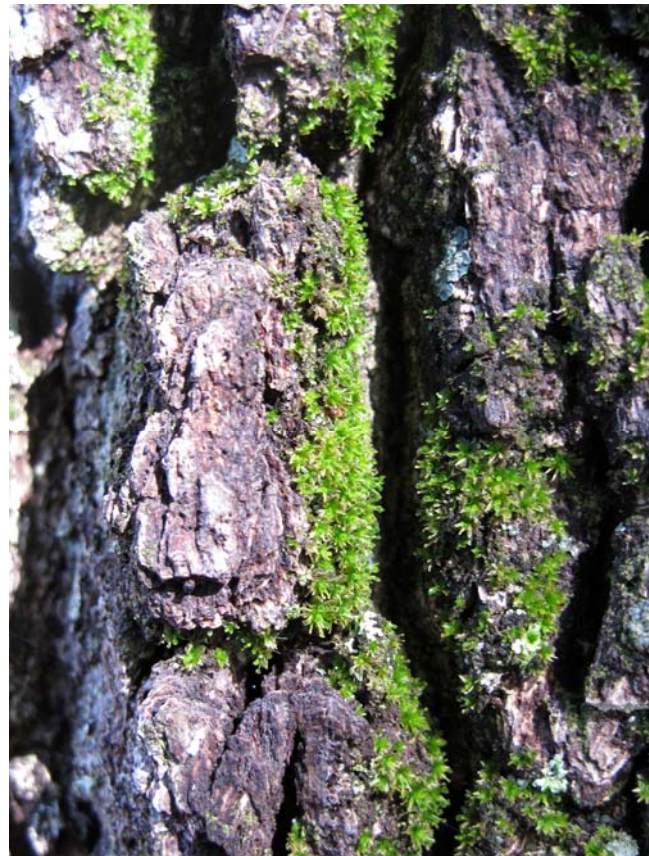


Figure 52. *Calymperes palisotii* on bark, a species that seems to be capable of anhydrobiosis in tropical Africa. Photo by Scott Zona, with permission.

Reproductive Biology and Phenology

As discussed earlier, the timing of reproduction must coincide with conditions favorable for dispersal. For example, both *Sematophyllum subpinnatum* (Figure 53) and *Octoblepharum albidum* (Figure 13) in the tropical Brazilian lowland forest have considerably more juvenile, immature, and mature gametangia during the rainy season than during the dry season, and that corresponds with an increase in the number of fertilized eggs in the archegonia

(Oliveira & Pôrto 2001; Pôrto & Oliveira 2002). One must keep in mind that unlike the desert, the dry season is subject to occasional, but short, rainfall events. In contrast to gametes, spores benefit from dry air for dispersal, and these two species derived that advantage by beginning sporophyte development during the rainy season, but completing it during the dry season.



Figure 53. *Sematophyllum subpinnatum*, a species that produces most of its juvenile, immature, and mature gametangia during the rainy season in tropical Brazil. Photo by Michael Lüth, with permission.

Despite our limited taxonomic knowledge, there have been several studies on the reproduction of tropical bryophytes. By their very nature, individual studies are limited to one or few species (*e.g.* Fatoba 1998). Nevertheless, Kürschner and Parolly (1998a, b), Kürschner *et al.* (1999), and Kürschner (2004) were able to review the life strategies and adaptations of bryophytes, noting that functional types are "important for the establishment, habitat maintenance, and dispersal of species," indicating relationships among site ecology, niche differentiation, and species evolution.

Bryophytes in tropical regions seem to have relatively fast population dynamics when compared to those of temperate species (Monge-Nájera 1989; Coley *et al.* 1993; Zartman 2004). This is often an adaptation to the ephemeral nature of many of their substrates.

Cerqueira *et al.* (2016) studied the seasonality of reproduction of epiphytic bryophytes in the flooded forests of the eastern Amazon. Of 54 species, 34 were fertile. They were unable to identify a pattern in the seven studied species when comparing those in dry vs rainy conditions. Two species, however, were associated with the seasonality. They concluded that some bryophytes may maintain constant fertility as an adaptation to these tropical forests.

Batista *et al.* (2018) found that in a humid forest in northeastern Brazil, with seasonal rainfall and dry season, the 76 bryophyte species were predominantly monoicous (67%) and exhibited reproductive traits that tolerated adverse conditions, permitting them to persist under the seasonal water availability of the forest. A total of 80% of the species had sporophytes, mostly among the monoicous species. Only 21% exhibited asexual reproduction,

including gemmae, regenerating fragments, and caducous leaves. Of these with asexual means, 75% were dioicous.

Life Cycle Strategies

Tropical forest substrata are usually rather temporary (Richards 1988), whether it be due to rapid decay, exfoliation, or soil erosion. In fact, Richards considers all substrata available to bryophytes in the tropics to be impermanent. Hence efficient short-distance dispersal is important. Epiphyllous species are frequently **colonists** with a short life span and production of numerous propagules. Species of *Fissidens* (Figure 71) and others that grow on termite mounds have a short-lived strategy. Richards (1988) carefully stated that the **perennial shuttle** with its relatively long life span and only moderate sexual or asexual reproduction is probably the commonest life strategy in the tropics, but that epiphylls are likely to be colonists because of the short duration of their substrate. **Fugitives** are rare, exceptions being the thallose liverwort *Riccia* (Figure 54) and the moss *Micromitrium* (Figure 55), as seen in West Africa.



Figure 54. *Riccia cavernosa*, a thallose liverwort; members of this genus are fugitives in West Africa. Photo by Des Callaghan, with permission.



Figure 55. *Micromitrium tenerum*; members of *Micromitrium* are fugitives in West Africa. Photo by Amelia Merced, with permission.

Mosses

The earliest of the tropical reproductive studies I could locate were those of Odu (1979, 1981). Studies on the mosses *Racopilum* (Figure 56) and *Fissidens* (Figure 71), indicate the importance of temperature in early life stages, with germination occurring at 30°C and protonema growth at 25°C (Odu 1979). This temperature requirement coincides with the maturation and dispersal of spores in the dry season, favoring the establishment of new shoots.



Figure 56. *Racopilum africanum*, a tropical species that relies on the rainy season for sexual reproduction. Photo by Jan-Peter Frahm, with permission.

Where seasons alternate between rainy and dry seasons, the rainy season is critical for completion of reproduction in species that rely on sexual reproduction. Odu (1981) demonstrated this for four species in southwest Nigeria, showing that release of spores was timed to take advantage of the dry season. The reproductive phenology of several tropical African mosses (*Racopilum africanum* (Figure 56), *Fissidens weirii* (see Figure 71; syn.=*F. glauculus*), *Pelekium gratum* (Figure 57; syn.=*Thuidium gratum*), *Stereophyllum* sp. (Figure 58) illustrate this. Using populations in southwestern Nigeria, Odu found that gametangia develop at the onset of the rainy season (March-April), whereas the development of sporophytes occurs later, with capsule maturation occurring at the end of the same rainy season (October-December). This permits dispersal of spores during and after the dry season (November-April). Thus the entire reproductive cycle is completed within one year. A similar relationship occurred among four species in a savannah in southwestern Nigeria (Makinde & Odu 1994).



Figure 57. *Pelekium gratum*, a tropical moss species that relies on the rainy season for sexual reproduction. Photo by Manju Nair, through Creative Commons.



Figure 58. *Stereophyllum radiculosum*, a tropical moss species that relies on the rainy season for sexual reproduction. Photo by Juan David Parra, through Creative Commons.

Both Olarinmoye (1974) and Egunyomi (1979a) determined that in studied bryophytes of west tropical Africa moisture is the regulatory factor for both growth and sporophyte production. Nevertheless, differences between species exist (Odu 1982). Odu found that *Fissidens weirii* (see Figure 71) and *Racopilum africanum* (Figure 56) have the shortest fertilization period, occurring in May. This fertilization period is earlier in *Pelekium gratum* (Figure 57) and much later in *Octoblepharum albidum* (Figure 13; Figure 59) (July-September). Nevertheless, the sporophytes of all four species mature toward the end of the rainy season (October-November). Herbarium specimens of these mosses collected over an 11-year period support this pattern.

Maciel-Silva and Oliveira (2016) examined the seasonal relationships of *Octoblepharum albidum* (Figure 13; Figure 59) in Brazil. Among 100 sporophyte-bearing plants, representing ten populations, the development was clearly seasonal, relating principally to rainfall. The early stages (immature to post-meiotic) occurred primarily during the dry season. Dehiscence, on the other hand, occurred mostly during the rainy season. This seems to be the opposite of that found for the species in Africa.

Octoblepharum albidum (Figure 59) is an autoicous pantropical species. Thus, its handling of various climatic regimes can help us to understand adaptations of reproductive strategies. Maciel-Silva *et al.* (2013) compared reproductive traits of this species in two Atlantic rainforests and two coastal sites in northeastern Brazil. This species not only produces spores frequently (Figure 59), but also produces gemmae at the leaf tips (Figure 60). In the coastal sites, the shoots had higher numbers of sporophytes, male and female branches per shoot, male gametangia per sexual branch, and longer setae than in the forest sites. Numbers of female gametangia per sexual branch did not differ between the two habitats and the male-biased sex ratio was present at all sites. Longer shoots produced more sporophytes, protonemata, and/or buds than did shorter ones, compared to production of gemmae, but only in the forest sites. The researchers suggested that the longer setae could favor spore dispersal, aiding colonization in coastal sites.



Figure 59. *Octoblepharum albidum* with capsules, a pantropical species that adjusts its reproductive strategies based on habitat climate. Photo by John Bradford, with permission.



Figure 60. *Octoblepharum albidum* with gemmae on the leaf tips. Photo by Li Zhang, with permission.

Oliveira and Pôrto (2005) examined sporophyte production and population structure of two moss species in the **Pottiaceae** in Brazil. Both *Hyophila involuta* (Figure 61) and *Hyophiladelphus agrarius* (Figure 62) produce capsules in the Atlantic forest at Recife, Pernambuco, Brazil (see Figure 63). Both species had a significantly female-biased sex ratio. The ratio of sterile to fertile shoots was close to 1:1. *Hyophila involuta* had a mean shoot density of 19 cm⁻², whereas it was 27 for *Hyophiladelphus agrarius*. Furthermore, *H. involuta* had only 48% sporophyte production, whereas *H. agrarius* had 55%. Neither species seemed to change its sporophyte production based on any of the environmental parameters measured. The males and females do not clump by sex, favoring sporophyte production.



Figure 61. *Hyophila involuta* with capsules. Photo by M. C. Nair, K. P. Rajesh, and Madhusoodanan, through Creative Commons.



Figure 62. *Hyophiladelphus agrarius* with capsules. Photo by Fred Essig, with permission.



Figure 63. Atlantic forest, Pernambuco coastal habitat, Camarigibe, Brazil. Photo by Leonardo Brito Uniemelk, through Creative Commons.

Antheridia and Archegonia

Pôrto and Oliveira (2002) did a more intensive study on the reproductive **phenology** (study of cyclic and seasonal natural phenomena) of *Octoblepharum albidum* (Figure 59) in the Atlantic Forest in Brazil. In this 2-year study, they found an average of 13.4 antheridia per **perigonium** (envelope of modified leaves surrounding antheridia) and 6.7 archegonia per **perichaetium** (ensheathing cluster of modified leaves surrounding archegonia). All stages of gametangia were much greater in the rainy season, with a concomitant increase in fertilized eggs in archegonia. The sporophytes began development during the rainy season and matured in the dry season, at which time spores were dispersed.

Even in the moss *Sematophyllum subpinnatum* (Figure 53), in which antheridia and archegonia initiate, mature, and achieve fertilization throughout the year, the frequency increases in the rainy season (Oliveira & Pôrto 2001). Sporophytes (see Figure 64) initiate primarily in June through September, indicating that the rainy season is the most favorable time for fertilization.



Figure 64. *Sematophyllum substrumosum* with capsules; capsules in *Sematophyllum subpinnatum* initiate in June through September in tropical Brazil, following fertilization in the rainy season. Photo by Michael Lüth, with permission.

Maciel-Silva and Valio (2011) found that in two different sites in the Brazilian rainforest, the phenology was somewhat different. Examination of eleven species of bryophytes indicates that the reproductive organs are active year-round. Female gametangia often mature before the onset of the rainy season. Male gametangia, however, tend to mature at the end of the dry season. Furthermore, at sea level, the highest production of immature male gametangia occurs at the start of the rainy season, whereas in the montane region, the highest production of immature male gametangia is at the end of the dry season. The researchers suggested that high temperatures could damage the development of male gametangia during the rainy season. Sporophytes dehisce before the rainy season begins, a time when spores can be dispersed farther by dry winds.

In summary, tropical gametangia mature primarily at the end of the dry season or beginning of the rainy season, most fertilizations occurs during the rainy season, and spore dispersal occurs during the dry season.

The pantropical moss *Sematophyllum subpinnatum* (Figure 53) is **autoicous** (having both sex organs on same plant but different branches) (Oliveira & Pôrto 2001). Sampling of two populations for two years in northeastern Brazil revealed that the average number of antheridia per perigonium ranges 9-20; archegonia per perichaetium ranges 3-26.

Monoicous vs Dioicous

As one might expect, **monoicous** (having both sexes on same plant) species have the highest levels of sporophyte production compared to **dioicous** (having sexes on separate plants) (Maciel-Silva *et al.* 2012a). Gradstein (1975, p. 29) found the highest level of sporophyte production in the autoicous *Acrolejeunea fertilis* (Figure 65) and *A. pycnoclada*, with a 15% presence of sporophytes in 100 collections of each of the two species studied. In other *Acrolejeunea* species mature sporophytes were present in less than 10% of collections studied, and sporophytes were not seen in two dioicous species. In their study of fertilizations in 11 species from a Brazilian Atlantic rainforest, Maciel-Silva and coworkers found that female-biased sex ratios and low rates of fertilization are typically balanced by high production of reproductive structures at the beginning of the reproductive cycle.



Figure 65. *Acrolejeunea fertilis*, an autoicous species with good sporophyte production. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for non-commercial use.

These same 11 species expressed sexual organs continuously over the 15-month period of study (Maciel-Silva & Valio 2011). Nevertheless, male gametangia are typically mature by the end of the dry season, with fertilization occurring during the wettest months. Female gametangia, on the other hand, are receptive over the entire period, with many maturing before the rainy season begins. Male gametangia experience a high abortion rate and take longer to develop. This pattern of male gametangia taking longer to develop is typical of bryophytes in many parts of the world. Sporophytes subsequently develop during the dry season, dispersing their spores toward the end of the season. Although the patterns of gametangia and sporophyte development differ among the species, it does not differ between the sea level and montane sites.

In Mexico, two dioicous species of *Syntrichia* [*S. fragilis* (Figure 66), *S. amphidiacea* (Figure 67)] are abundant (Mishler 1988). Both produce sporophytes only in limited circumstances within their range. Nevertheless, they are just as abundant in areas where sporophytes are rare or absent. This suggests that they must rely heavily on asexual reproduction in these areas.



Figure 66. *Syntrichia fragilis* dry, an abundant dioicous species in Mexico, but seldom producing capsules. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 67. *Syntrichia amphidiacea* dry, an abundant dioicous species in Mexico, but seldom producing capsules. Photo by Claudio Delgadillo Moya, with permission.

Propagules and Regrowth

Some widespread tropical bryophytes do not produce capsules and spores, usually due to absence of the opposite sex, poor gamete dispersal, or unsuccessful development of the sporophyte. Olarinmoye (1986) examined survival strategies of the mosses *Hyophila crenulata* (see Figure 68), *Barbula lambarenensis* (see Figure 69-Figure 70), and *Fissidens asplenioides* (Figure 71) in Ibadan, Nigeria. He established that survival strategies during unfavorable periods of drought could be as spores (only in *Hyophila crenulata*), gemmae, and regrowth from the gametophores, as well as regrowth from rhizoids, shoot bases, apices, and the main stem. Rhizoids produce more regrowth than do shoot apices and main stems. He considered the production of spores in *H. crenulata* to give it a competitive advantage. Nevertheless, the gemma production and success of the other two species seems to more than compensate for lack of spores, as witnessed by their abundance and widespread distribution there.



Figure 68. *Hyophila involuta* (Pottiaceae) with capsules; *Hyophila crenulata* survives dry periods by spores, gemmae, and regrowth from any of its gametophore parts. Photo by Michael Lüth, with permission.



Figure 69. *Barbula horrinervis* (Pottiaceae) with bulbils in leaf axils; *B. lambarenensis* survives dry periods by gemmae that serve the same function as bulbils. Photo by Michael Lüth, with permission.



Figure 70. *Barbula tenuirostris* (Pottiaceae) showing broken leaves that could regenerate; *B. lambarenensis* uses such fragments to regrow following drying out. Photo by Michael Lüth, with permission.



Figure 71. *Fissidens asplenioides*, a species that survives following drought through regrowth from various plant parts. Photo by Jan-Peter Frahm, with permission.

Propagule Forms

Tropical moss gemmae do not seem to have the same limited number of forms as do liverwort gemmae. Odu (1987) found a "great multiplicity of forms" among the gemmae in tropical West African mosses. These occur in a variety of locations, including leaf and leaf axils, and sometimes occur in more than one type of location. Odu concluded that gemmae are of "immense ecological importance" to the tropical mosses. This is facilitated in **Calymperaceae** (Figure 52) by rapid germination – within 1-2 days after becoming dislodged from the leaves. In **Bryaceae**, asexual propagules are often produced as multicellular rhizoidal tubers (Figure 72). In addition to these, there may be gemmae in leaf axils and on rhizoids. As in **Calymperaceae**, gemma germination is rapid, within 2-3 days. In southern Nigeria, some species of **Pottiaceae** (Figure 68-Figure 70) have few male plants and hence rely on gemmae.



Figure 72. *Bryum dichotomum* rhizoidal tuber, a common means of reproduction in West Tropical Africa. Photo by Des Callaghan, with permission.

Calymperes (Figure 52) is one of the prominent gemmiferous mosses in the tropics. When examining *C. afzelii* (Figure 73) and *C. erosum* (Figure 74) Odu and Owotomo (1982) found that the shoots are **dimorphic** (having two forms). That is, the first leaves to develop do not produce gemmae. Later leaves are gemmiferous (Figure 74), and these alternate in coordination with the dry and rainy seasons.



Figure 73. *Calymperes afzelii*, a species that produces protonemata and single-layered gemmae in leaf axils. Photo by Piers Majestyk, through Creative Commons.



Figure 74. *Calymperes erosum* with gemmae; this species does not produce gemmae on its first shoots. Photo by Li Zhang, with permission.

Egunyomi (1984) surveyed the asexual **diaspores** (propagule; any structure that functions in plant dispersal) of mosses in Nigeria. He recognized two major categories: caducous shoots and gemmae. Species with one or more of these asexual diaspores comprise 15% of the Nigerian moss flora. He considered this means of reproduction to be especially important for mosses that do not produce sporophytes in all or part of their range. Seven of these species are sexually sterile.

The miniature **caducous** (can break away from the stem) shoots are often found with rhizoids (Egunyomi (1984)). Species with this type of diaspore include *Trachycarpidium tisseranti* (see Figure 75), *Archidium* sp. (Figure 76), *Bryum argenteum* (Figure 77), *B. coronatum* (Figure 78), *Bryum nitens*, and *Campylopus* (Figure 79) species. The latter two are strongly caducous.

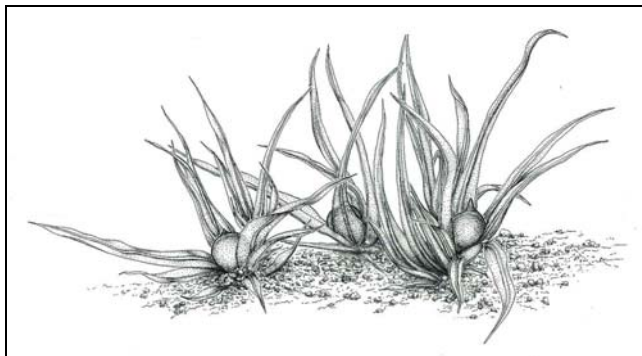


Figure 75. *Trachycarpidium brisbanicum*; *Trachycarpidium tisseranti* has caducous shoots that aid its dispersal in tropical Africa. Drawing by Rod Seppelt, with permission.



Figure 76. *Archidium alternifolium*, a species with caducous shoots. Photo by Jan-Peter Frahm, with permission.



Figure 77. *Bryum argenteum*, a species with caducous shoots. Photo by Tushar Wankhede, through Creative Commons.



Figure 78. *Bryum coronatum*, a species with caducous shoots. Photo by Michael Lüth, with permission.



Figure 79. *Campylopus subulatus* with broken tips that become dispersal units. Photo by David T. Holyoak, with permission.

The second type is the **gemma** (Egunyomi 1984). In some, these are **uniseriate** (having only one cell layer) and produced from protonemata in leaf axils. This type includes *Splachnobryum gracile* (see Figure 80), *Jaegerina scariosa* (Figure 81), *Henicodium geniculatum* (Figure 82), and *Bryum argenteum* (Figure 77). Production of rhizoidal gemmae in *Splachnobryum gracile* and *B. argenteum* seems to be related to the high humidity where they were collected. Another type of gemma is borne on **excurrent** (extending beyond leaf tip) **costae** (leaf rib) and is **clavate** (club-shaped, like a baseball bat). Species with these include *Calymperes erosum* (Figure 74), *C. afzelii* (Figure 73), *C. palisotii* (Figure 52), and *C. rabenhorstii*. *Calymperopsis martinicensis* produces filamentous gemmae that occur in splash cups at the shoot apex. In *Octoblepharum albidum* (Figure 13), the gemmae occur at leaf apices and along the margins. Multiseriate gemmae occur in *Semibarbula lambarenensis* and *Hyophila crenulata* (see Figure 61). *Gemmabryum apiculatum* (see Figure 83-Figure 85), and *Anoetangium spathulatum* (see Figure 86) produce **tubers** (Figure 85). These tubers are present on rhizoids in the soil and can germinate when the soil is disturbed. This can occur when wet season rains first disturb the soil. Tubers are able to remain viable 9-12 months after collection.



Figure 80. *Splachnobryum obtusum*; *Splachnobryum gracile* produces rhizoidal gemmae in the tropics. Photo from British Bryological Society, with permission.



Figure 81. *Jaegerina scariosa*, a species that produces protonemata and single-layered gemmae in leaf axils. Photo courtesy of Lucas Matheus da Rocha.



Figure 82. *Henicodium geniculatum*, a species that produces protonemata and single-layered gemmae in leaf axils. Photo by Piers Majestyk, through Creative Commons.

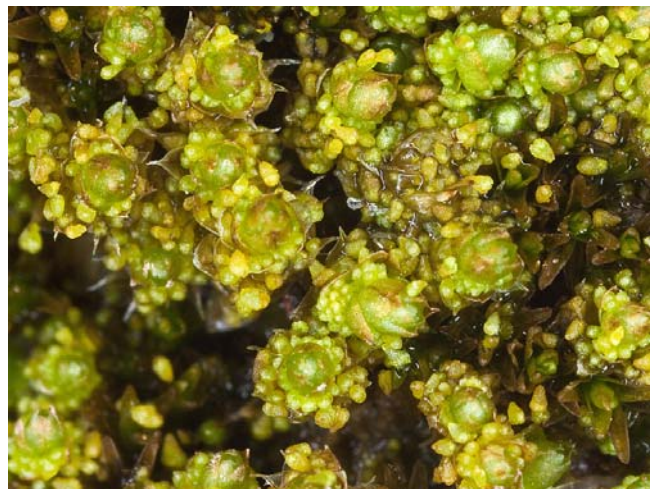


Figure 83. *Gemmabryum dichotomum*; *Gemmabryum apiculatum* is a species with both bulbils and tubers. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

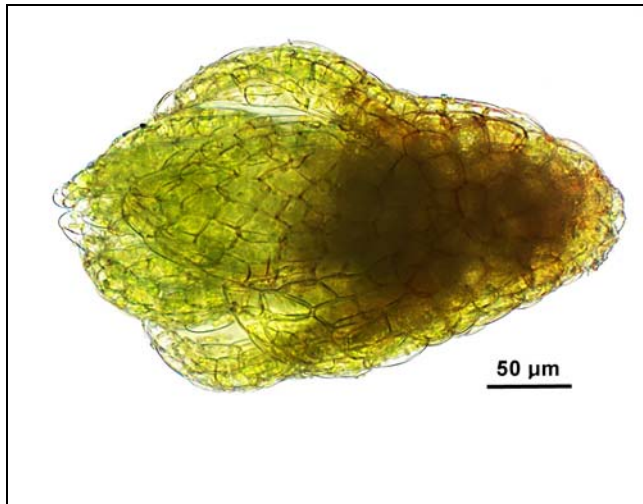


Figure 84. *Gemmabryum dichotomum* bulbil. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

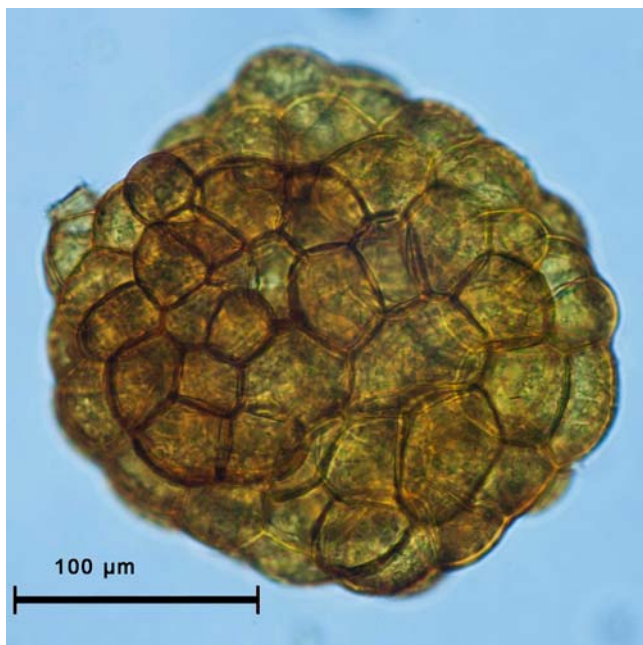


Figure 85. *Gemmabryum apiculatum* tuber. Photo by Jan Janssens, with permission.



Figure 86. *Anoetangium aestivum*; *Anoetangium spatulatum* produces tubers in the tropics. Photo by Hermann Schachner, through Creative Commons.

Fragments

In many cases throughout the world, fragments of bryophytes are important in producing new colonies [see, for example, *Octoblepharum albidum* (Figure 13) Egunyomi *et al.* 1980]. Nadkarni *et al.* (2000) tested the interception and retention of bryophyte fragments on branches in a tropical montane cloud forest in Costa Rica. They found that for canopy-dwelling tracheophytes, establishment of bryophytes frequently occurs first. Most fragments don't succeed in becoming established, but about 1% do adhere and become established when dropped from above. On the other hand, 24% were retained among undisturbed bryophytic epiphytes during the 6-month study and 5% were retained on stripped branches.

Spore Size

Richards (1984a) found that sun epiphytic mosses usually have larger spores than do shade epiphytes. This would provide a better energy source for the establishment of the sun mosses, whereas the shade mosses would have a better opportunity for dispersal. Spore size seemed to be unimportant among the liverworts, but van Zanten and Gradstein (1988) determined that some shade liverwort epiphytes had spores with much less drought resistance, failing germination after only a few days of desiccation. This lack of drought resistance greatly limits the dispersal range.

Diaspore Banks

Diaspore (structure that functions in plant dispersal; propagule) banks provide temporary refuge for spores, gemmae, and sometimes fragments, particularly in habitats that are frequently dry (During & Moyo 1999).

Egunyomi (1979b) tested longevity of spores from Nigeria by keeping them at room temperature and humidity for 1-3.5 years. Subsequent germination ranged from 0 to 92%. Fifteen of 21 species had no germination after that time. Only four species [*Weisiopsis nigeriana*, *Microcampylopus nanus* (see Figure 87), *Mittenothamnium overlaetii* (see Figure 88), *Weissia papillosa* (see Figure 89)] had at least 50% germination after two years. *Calymperes erosum* (Figure 74) survived at least 1 year with 71% germination. *Microcampylopus nanus* and *Weissia papillosa* had 75 and 76% survival, respectively, of alternate wetting and air drying every 24 hours for four weeks following two years of desiccation. None of the four species with 50% germination listed above survived 4 weeks at -2° following 2 years of desiccation. All four species had at least 43% survival for 4 weeks at 8°C following 2 years of desiccation, with *Microcampylopus nanus* having 80% and *Weissia papillosa* having 81%. Continuous submersion in water was as detrimental as freezing, with none of the four species surviving up to 3 weeks and the highest survival after one week was only 31% (*Weissia papillosa*). Egunyomi suggested that the submersion led to deterioration of the spores due to fungal attack.



Figure 87. *Microcampylopus laevigatus*; *M. nana* can germinate from spores after two years of storage. Photo by Jan-Peter Frahm, with permission.



Figure 88. *Mittenothamnium reptans* from the Neotropics; *M. overlaetii* can germinate from spores after two years of storage. Photo by Michael Lüth, with permission.



Figure 89. *Weissia rutilans* with capsules; *Weissia papillosa* can germinate from spores after two years of storage. Photo by Michael Lüth, with permission.

Zander and During (1999) described a new species of the moss family **Pottiaceae** – *Neophoenix matoposensis* (Figure 90) from the diaspore bank of an experimental fire plot in Zimbabwe. They noted that diaspore banks often harbor the small species with a short life cycle that make

them difficult to find above ground. In addition, they found the accompanying species *Bryocephospora aethiopica* (Figure 91) (new to Zimbabwe) and *Uleobryum occultum* (Figure 92) (new to Africa, a species formerly known only from Brazil and Australia).



Figure 90. *Neophoenix matoposensis*, a new species discovered from a diaspore bank in Zimbabwe. Image modified from drawing by Patricia Eckel in Zander & During 1999.



Figure 91. *Bryocephospora aethiopica* with capsules, a species known from diaspore banks in Zimbabwe. Photo by Claudio Delgadillo Moya, with permission.



Figure 92. *Uleobryum occultum*, a species known from diaspore banks in Zimbabwe. Photo by Claudio Delgadillo Moya, with permission.

Maciel-Silva *et al.* (2012b) examined the properties of diaspore species in diaspore banks in the tropical rainforests. They compared species from the Atlantic rain forest (montane and sea level) in Brazil. Of the species identified, 68 were from bark, 55 from decaying wood, and 22 from soil. These species numbers differed little between sites. Mosses predominated, and monoicous species were more numerous than dioicous species. There was little pH effect on shoot emergence. The extant vegetation was well represented, with gemmae and spores making a high contribution. The researchers postulated that the diaspore banks contribute to fast establishment of species after disturbance of the tropical rainforests, as well as contributing to succession there. This is particularly true for species that produce lots of gemmae or monoicous mosses with a large commitment to sexual reproduction.

Bisang *et al.* (2003) germinated diaspores from Malaysian soil. Many of the germinated plants could not be identified and lived only a short time. Two moss species germinated from stem fragments – *Isopterygium* (Figure 93) and possibly *Ectropothecium* (Figure 94). The diaspore origin of the third identifiable moss, *Calymperes* (Figure 52), could not be determined.



Figure 93. *Isopterygium tenerum*; the genus *Isopterygium* was among those that germinated from diaspore banks in the Malaysian mountain rainforest. Photo by Scott Zona, with online permission.



Figure 94. *Ectropothecium* sp., a genus tentatively identified among those that germinated from diaspore banks in the Malaysian mountain rainforest. Photo by Niels Klazenga, with permission.

Diaspore banks can be especially important after a major disturbance such as a fire (During 1998, 2007). In his study in southern Zimbabwe, During found emergence of 2 hornworts, 10 liverworts, and 22 mosses from surface soil samples of the savannah Matopos Sandveld Fire Plots. Annual burning did not seem to harm the diaspores hidden in the soil.

Conditions are not good for sexual reproduction in the tropics. Even if the plant has successful fertilization, sporophyte maturation and dispersal might not be successful. For example, in *Bryum coronatum* (Figure 78), sporophytes are common in Nigeria (Egunyomi 1982). Nevertheless, Egunyomi found 42% of the capsules remained undehiscent even in the dry season. Furthermore, 41% of the setae had no capsules. On the other hand, spore germination was successful 65-88% of the time, but the protonemata exhibited abnormal growth. Egunyomi suggested that the numerous axillary propagules were important in dispersal in this species.

Prolonged Protonemal Stage

One adaptation to the short growth period is to prolong the duration of the protonema. As Gradstein and Wilson (2009) put it, this can be interpreted as a short-cut in the life cycle that permits rapid maturation and reproduction, both providing benefits in unstable, impermanent habitats. In this extreme, it is known as **neoteny**. The most extreme of these are in bryophytes that produce capsules directly on the protonema. The thalloid type occurs only among epiphyllous bryophytes. In the tropics, the epiphytic moss *Ephemeropsis* (Figure 95-Figure 96) produces persistent thalloid protonemata.



Figure 95. *Ephemeropsis trentepohlioides* with capsules. Photo by David Tng, with permission.



Figure 96. *Ephemeroopsis tjibodensis* protonematal mat on palm in Fiji. Photo by Tamás Pócs, with permission.

Liverworts

Liverworts in general produce gemmae more commonly than do mosses. And many of them are more sensitive to desiccation and low humidity. This leads to some differences in their adaptations to living in the tropics.

Monoicous vs Dioicous

Schuster (1988) surmised that sexuality of liverworts shifts to **monoicous** (both sexes on same plant) in the tropics, with *Plagiochila* (Figure 97) being a notable exception as entirely **dioicous** (sexes on separate plants). Schuster considers the ability of monoicous taxa to easily achieve fertilization to be an advantage on impermanent substrata such as leaf surfaces, twigs, and even tree trunks.



Figure 97. *Plagiochila* sp., a dioicous tropical leafy liverwort. Photo by Lin Kyan, with permission.

Neoteny

The monoicous property is further enhanced by multiple examples of **neoteny** (ability of juvenile plants to

reproduce, e.g. species of *Cololejeunea* (Figure 98-Figure 100), a condition known for liverworts only in the tropics (Schuster 1988; Gradstein *et al.* 2006). Gradstein and Wilson (2009) note that botanists have interpreted neoteny as a short-cut in the life cycle because it permits rapid maturation and reproduction, an advantage in unstable, impermanent habitats. This is especially important for those species, like *Cololejeunea* species, that live on such temporary substrata as leaves (Schuster 1988; Gradstein *et al.* 2006). The high level of reproduction, especially sexual reproduction, coupled with the high diversity of niches in tropical forests, has resulted in a large number of liverwort taxa. In some cases, the leafy liverwort gametophyte is replaced by a large and persistent protonema (Figure 100) (Gradstein & Wilson 2009).



Figure 98. *Cololejeunea minutissima*; members of *Cololejeunea* exhibit neoteny in the tropics. Photo by Michael Lüth, with permission.

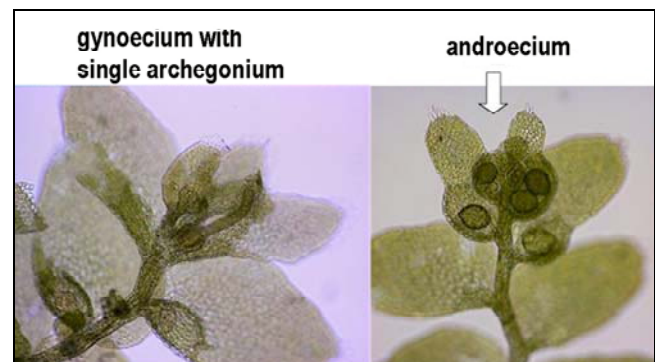


Figure 99. *Cololejeunea cardiocarpa* archegonium and antheridia exhibiting neoteny. Photo by Paul Davison, with permission.

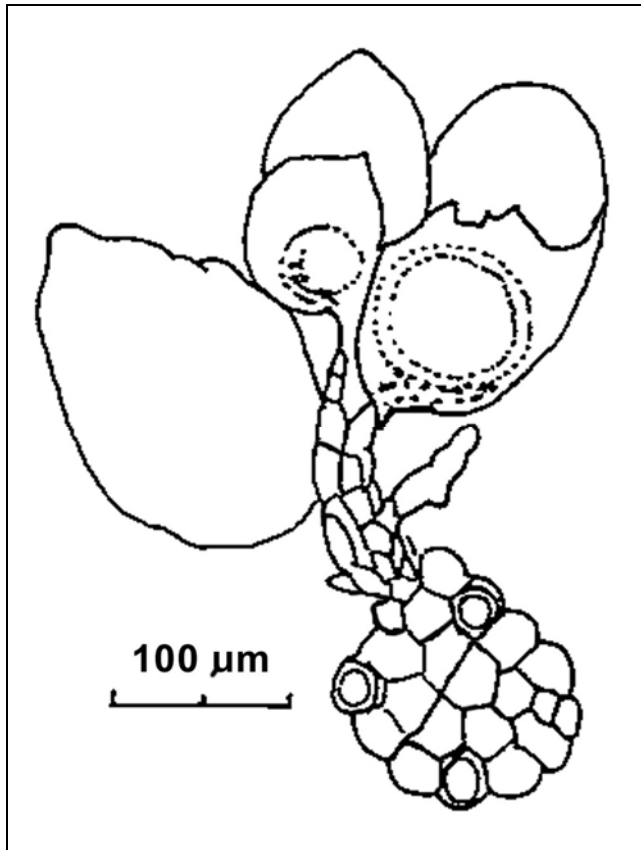


Figure 100. *Cololejeunea borhidiana* dwarf male, an extreme case of neoteny. Image by Tamás Pócs, slightly modified, with permission.

Reduced Numbers of Antheridia and Archegonia

Many temperate liverwort taxa produce numerous antheridia (5-16) and archegonia (12-25) (Schuster 1988). This is wasteful since only one archegonium on a branch can successfully produce a sporophyte. In tropical liverworts, these numbers are reduced to a more typical 1-4 archegonia and 1-2 antheridia per set of bracts (Figure 99). Furthermore, the size of gametangial branches is reduced (Figure 100) in many tropical taxa. Since gametes are typically released during the wet season, the danger of their drying out without achieving fertilization is reduced.

One rather unusual tropical leafy liverwort is *Colura irrorata* (Figure 101), a **rheophilous** (thrives in running water) member of **Lejeuneaceae** that grows part of the year submerged in torrential water (Figure 101). It was long known only from the banks of the Rio Topo in the Pastaza province of Ecuador (Thiers 1988) where it was discovered by Richard Spruce in 1857. It was long considered extinct until it was rediscovered there by Gradstein *et al.* (2004). A second locality of the rare species, in the same type of habitat, was recently found several hundreds of km further to the south in Ecuador (Gradstein & Benitez 2014). The species is more robust and has a more complex structure than other members of the **Lejeuneaceae**, but its most outstanding feature is its reproduction. Thiers (1988) estimated that a 2-cm section of stem could produce as many as 1600 **gynoecia** (archegonia and surrounding bracts, *i.e.* female reproductive structures).



Figure 101. *Colura irrorata*, a species that produces up to 800 gynoecia per cm. Photo by Lou Jost, through Robbert Gradstein.

Short Life Cycles

These tropical liverworts enjoy short life cycles (spore to spore), with epiphyllous species completing a full cycle in one year and those on other substrata in 2-3 years (Schuster 1988; Piippo 1992). This is enhanced by green spores (Figure 102) that are able to germinate immediately, and that predominantly germinate within the capsule (Schuster 1988). Despite these indicators that long-distance dispersals are unlikely, there is ample evidence that at least some of them are successful.

One example of the spore germination for a common tropical species is that of the leafy liverwort *Frullania ericoides* (Figure 102-Figure 103) (Silva-e-Costa *et al.* 2017). This species is **endosporic** (spores divide within spore wall), producing a globular protonema within the spore wall. By the fourth week, the protonema breaks through the spore wall and produces tightly concave primordial leaves. This germination occurs at 1/4, 1/2, full, and 1 1/2 strength Knop's nutrient solution, but fails to occur at double strength solution. This suggests that nutrient requirements for successful germination are relatively low (compared to that of tracheophytes) and that nutrient-rich substrates would be detrimental to these liverworts.

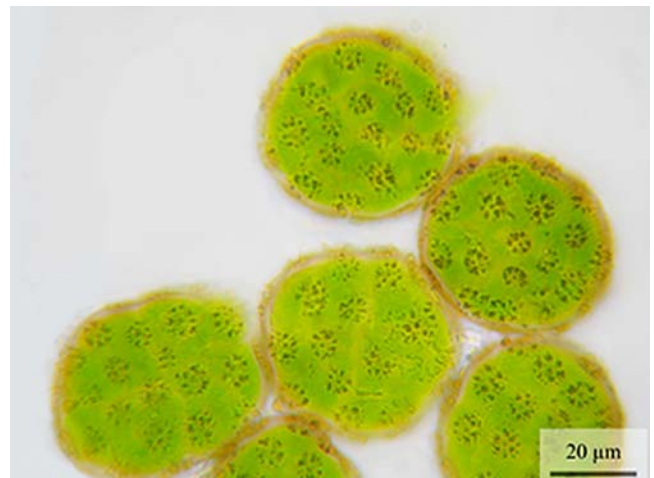


Figure 102. *Frullania ericoides* endospores, demonstrating their green color and germination within the spore. Photo from da Costa Silva-e-Costa *et al.* 2017, through Creative Commons.

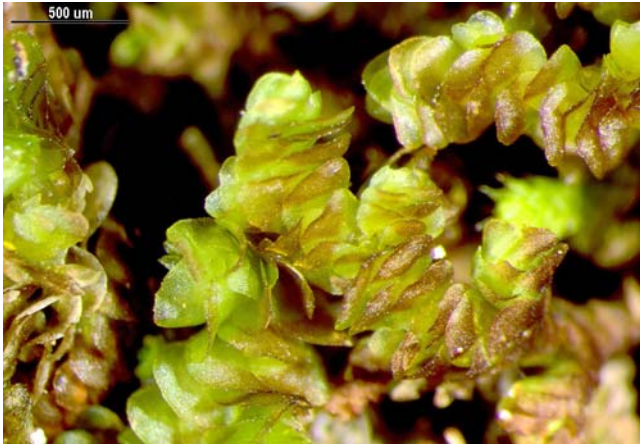


Figure 103. *Frullania ericoides*, a common tropical leafy liverwort. Photo by Blanka Aguero, with permission.

Alfayate *et al.* (2013) examined the spores of four pleurocarpous mosses in the Canary Islands, islands with a subtropical climate. They found that two of these were **isosporic** (all spores same size), but *Leucodon canariensis* (Figure 104) had two size classes of spores: medium-sized 1-celled spores and large multicellular spores. Furthermore, *Cryptoleptodon longisetus* (see Figure 105-Figure 106) has two sizes of spores, small spores and medium-sized spores. Spores germinate within the capsules in three of these species: *Leucodon canariensis*, *Cryptoleptodon longisetus*, and *Neckera intermedia* (Figure 107). *Neckera cephalonica* (Figure 108) spores do not germinate in the capsule. The perine wall of the spores of these species is papillose, an uncommon character for spores. The spores contain abundant lipid-like structures and chloroplasts with well-developed thylakoids.



Figure 104. *Leucodon canariense*, a species with two spore sizes: medium-sized 1-celled spores and large multicellular spores. Photo from BBS website, with permission from Barry Stewart.



Figure 105. *Cryptoleptodon* sp. in its habitat in India. Photo by Michael Lüth, with permission.



Figure 106. *Cryptoleptodon* sp. *Cryptoleptodon longisetus* is a species with two sizes of spores. Photo by Michael Lüth, with permission.



Figure 107. *Neckera intermedia*, a species with spores that germinate in the capsule. Photo by Jan-Peter Frahm, with permission.



Figure 108. *Neckera cephalonica*, a species with spores that do not germinate in the capsule. Photo by Jan-Peter Frahm, with permission.

Short Spore Longevity

Tropical liverwort spores have a short longevity and are unable to survive desiccation (Schuster 1988). Rather, they have several adaptations for rapid germination. They are typically **endosporic** (germinating and beginning development within spore wall; Figure 102), spores germinate within the capsule, and spores have elastic walls to facilitate development.

Prolonged Protonemal Stage

Several liverworts have remarkably prolonged protonemal stages, as in *Radula yanoella* (Figure 109) from the Amazonian rainforest (Thiers 1988; Gradstein & Wilson 2009). This species has since been found in French Guyana, Ecuador, and Costa Rica (Gradstein & Ilkiu-Borges 2009). In *Protocephalozia ephemeroides* (Figure 110) and *Cololejeunea metzgeriopsis* (Figure 111-Figure 112; syn.=*Metzgeriopsis pusilla*), the protonemal stage replaces the leafy gametophyte except in association with the reproductive structures (Gradstein *et al.* 2006). *Metzgeriopsis pusilla* was formerly considered the only species in its genus, but has since been placed in *Cololejeunea* as *C. metzgeriopsis* (Gradstein & Wilson 2009). It lives in humid montane forests of tropical southeast Asia, growing as an epiphyll on living leaves. Its thallus is unistratose with minute, leafy sexual branches arising from the margins. *Protocephalozia ephemeroides* is a very rare liverwort, known only from two localities in southern Venezuela, near the border with Brazil, where it was collected by Richard Spruce. There it was growing on moist earth in shade and on little mounds "thrown up by mud worms." Thiers (1988) suggests that the normally short-lived liverwort protonemal stage has been lost in these taxa, replaced by a long one, because of the always abundant moisture. The protonemal stage of most bryophytes is typically subject to damage from rapid drying. This protonema can be thalloid, as in the liverworts *Cololejeunea metzgeriopsis* (Figure 112) and *Radula yanoella* (Figure 109), or filamentous, as in the leafy liverwort *Protocephalozia* (Figure 110) (Gradstein & Wilson 2009).

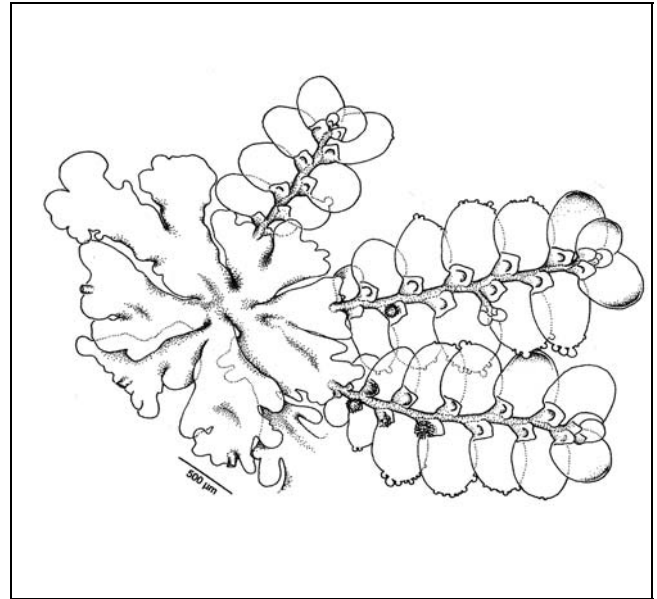


Figure 109. *Radula yanoella*, a leafy liverwort with a remarkably prolonged thalloid protonema. Drawing courtesy of Robert Gradstein, from Gradstein and Ilkiu-Borges 2009.

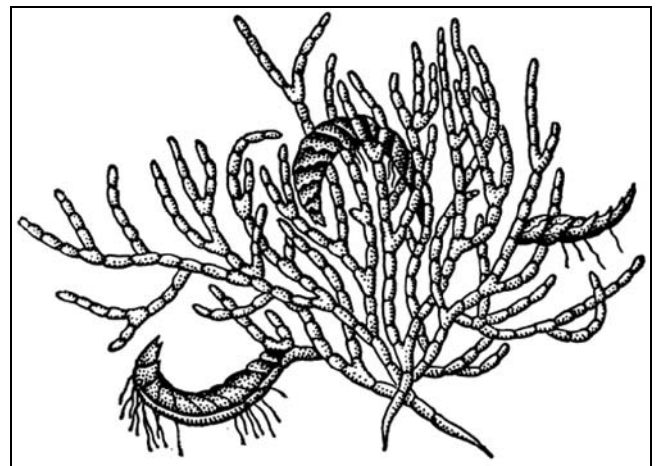


Figure 110. *Protocephalozia ephemeroides* with protonema and male gametophores. Image from Plantlife.ru, with implied online permission.

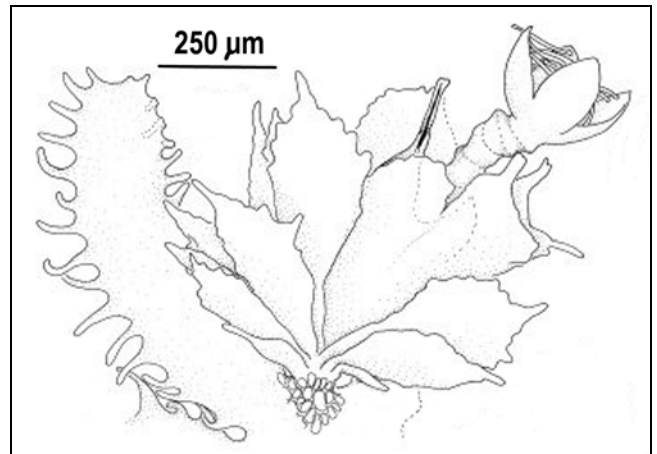


Figure 111. *Cololejeunea metzgeriopsis* plant with female organ. Drawing modified from Gradstein *et al.* 2006, with permission.

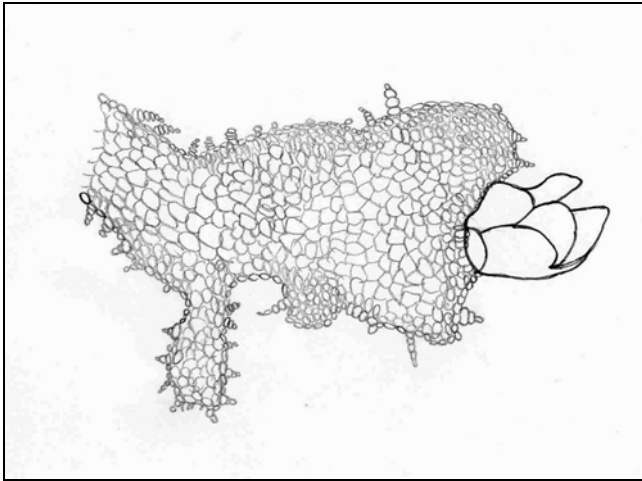


Figure 112. *Cololejeunea metzgeriopsis* protonema. Drawing by Žofie Juříčková, through Creative Commons.

Types of Gemmae

Even gemmae differ between the tropics and temperate zones (Schuster 1988). In temperate zones, the commonest types of gemmae are 1-2 cells and occur in branching chains (Figure 113). As such, they are easily dispersed, much like spores. These small gemmae occur in the **Jungermanniales** [e.g. **Cephaloziaceae** (Figure 114), **Calypogeiaceae** (Figure 115-Figure 116), **Scapaniaceae** (Figure 117-Figure 119), **Lophoziaceae** (Figure 120-Figure 122), **Cephaloziellaceae** (Figure 123-Figure 124)]. A single shoot can produce thousands of gemmae in a single growing season. This type of gemma is not so common in the tropics, where the more common **Porellales** (including **Lejeuneaceae**; Figure 125-Figure 126) have large gemmae. Instead, many tropical species tend to have discoid and single-layered gemmae, permitting easy dispersal to "considerable distances." The number of types is more limited, including discoid gemmae (Figure 126) and **caducous** (deciduous) branches (Figure 127). Even fragmenting branches are rare in the tropics. Gemmae are in general less common and less important among sexually reproducing tropical liverworts, even though many liverworts may produce both gemmae and sexual organs.



Figure 113. *Nowellia curvifolia* leaf gemmae, demonstrating the branching chains of 1-2-celled gemmae. Photo by Paul Davison, with permission.



Figure 114. *Odontoschisma longiflorum* (Cephaloziaceae) from the Neotropics, showing the small, branched chains of gemmae. Photo by Michael Lüth, with permission.



Figure 115. *Calypogeia muelleriana*, with clusters of gemmae. Photo by David T. Holyoak, with permission.

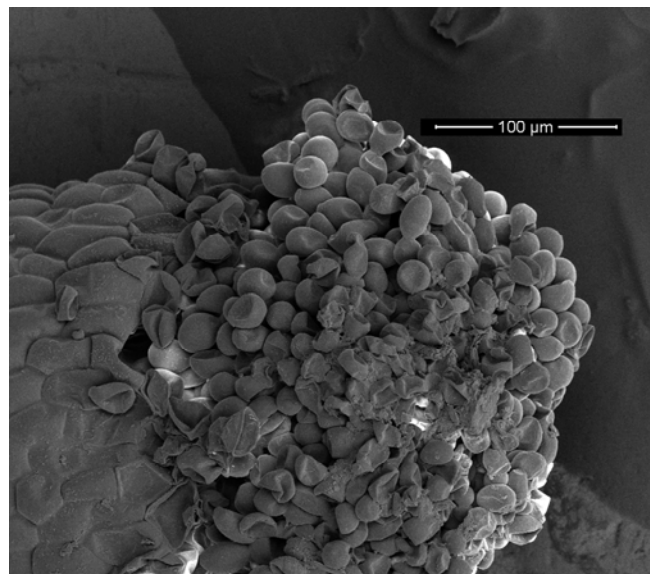


Figure 116. SEM of *Calypogeia muelleriana* leaf with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 117. *Diplophyllum albicans* (Scapaniaceae), a species with worldwide distribution that includes the tropics. Photo by J. C. Schou, with permission.



Figure 120. *Lophozia ventricosa*, a widespread species that occurs in the Neotropics. Photo by Hermann Schachner, through Creative Commons.

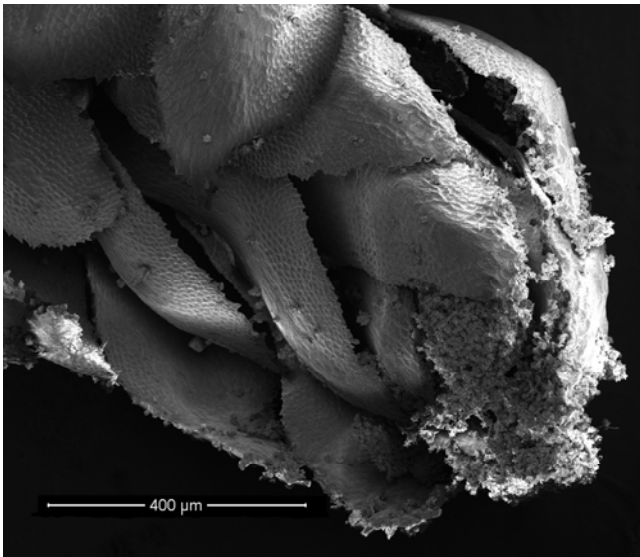


Figure 118. SEM of *Diplophyllum albicans* leaves with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

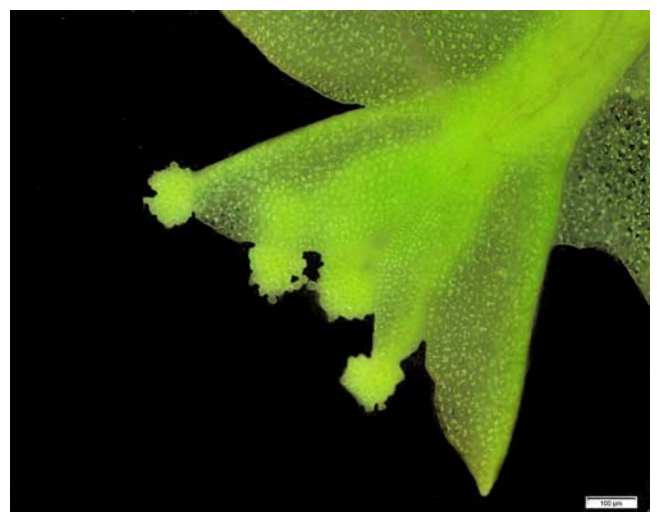


Figure 121. *Lophozia ventricosa* with gemmae on the leaf tips, a species found in the Neotropics. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

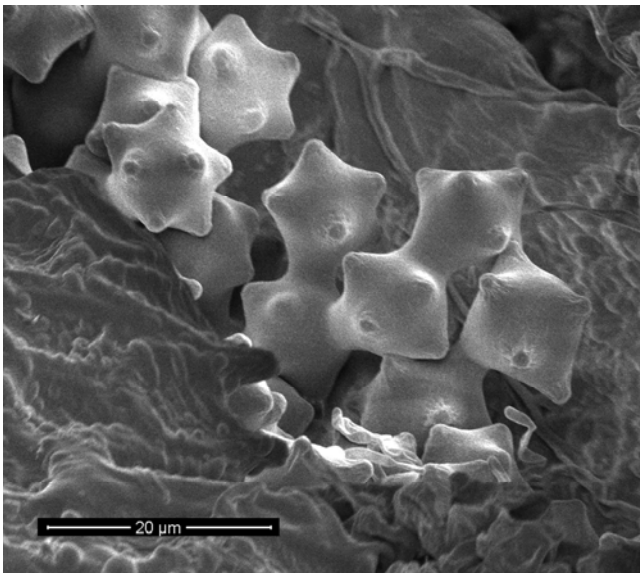


Figure 119. SEM of *Diplophyllum albicans* gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

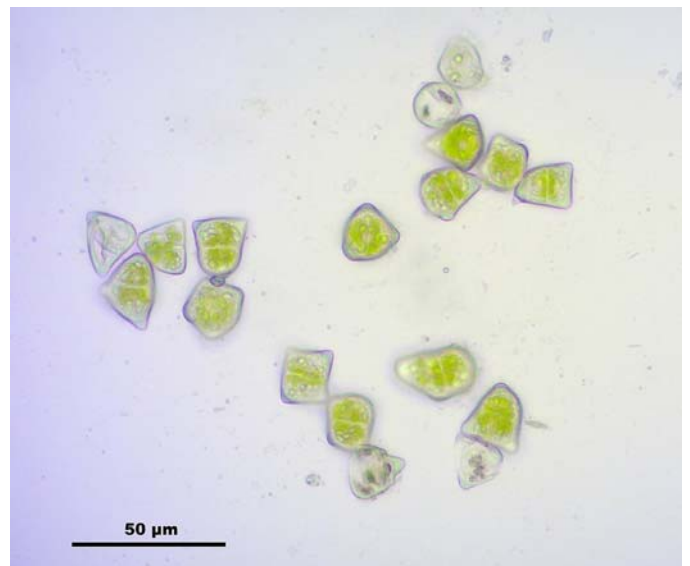


Figure 122. *Lophozia ventricosa* gemmae. Photo by Hermann Schachner, through Creative Commons.



Figure 123. *Cephaloziella bicuspidata* (Cephaloziellaceae). Photo by Botany Website, UBC, with permission.

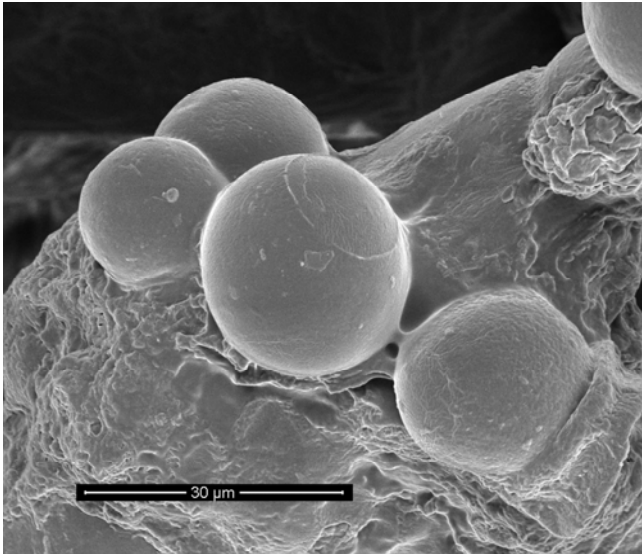


Figure 124. SEM of *Cephaloziella bicuspidata* gemmae, demonstrating the small gemma size of the Cephaloziellaceae. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 125. *Cololejeunea cardiocarpa* (Lejeuneaceae), a leafy liverwort that occurs in the tropics and has large gemmae. Photo by Blanka Agüero, with permission.

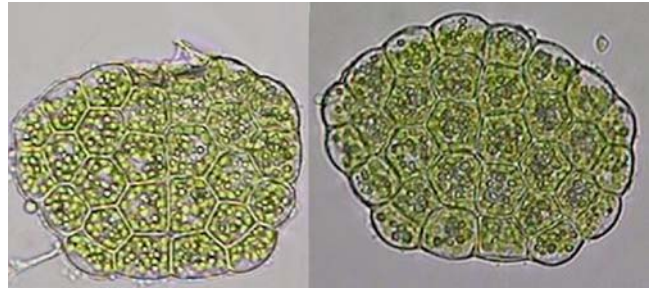


Figure 126. *Cololejeunea cardiocarpa* gemmae, showing the large gemma size typical of the Lejeuneaceae. Photo by Paul Davison, with permission.



Figure 127. *Prionolejeunea saccatiloba* showing small, caducous branch that can fall off for asexual reproduction. Photo by Michaela Sonnleitner, with permission.

Another anomaly among tropical liverworts is that gemmae and sexual organs can be produced at the same time, as in many species of *Cololejeunea* (Figure 125-Figure 126, Figure 128-Figure 129) (Schuster 1988). By contrast, in temperate regions many species of **Lophoziaceae** and **Scapaniaceae** (Figure 130) may produce gemmae and sex organs at the same time. Their gemmae are typically produced in response to submarginal growth conditions that would often suppress production of sex organs.



Figure 128. *Cololejeunea minutissima*; many species in this large genus produce gemmae and sexual organs at the same time. Photo by David T. Holyoak, with permission.



Figure 129. *Cololejeunea truncatifolia* from Uganda; many species in this genus produce gemmae and sexual organs at the same time. Photo by Martin Wigginton, with permission.



Figure 130. A temperate one *Scapania nemorea* with gemmae. Some temperate populations of *Scapania* can at times produce sexual structures and gemmae at the same time. Photo by Dick Haaksma, with permission.

Van Zanten and Gradstein (1987) found that spores of endemic liverwort species had less resistance to drying and freezing than did the transoceanic species of Colombian liverworts. When subjected to intercontinental transport on the wing tips of a jet airplane, spores of 60 out of 61 species became inviable, presumably due to high UV levels at jet stream levels. Only spores of two species growing at high elevation (ca. 4000 m) were able to germinate after the flight. Probably they were well-adapted to UV radiation. On the other hand, van Zanten and Gradstein found that wet freezing permitted survival. They suggested that liverworts from high altitudes had a "good possibility" for aerial long-distance dispersal through hurricanes and tropical storms.

Diaspore Banks

Bisang *et al.* (2003) cultured diaspores from three Malaysian mountain rainforests. They found that more liverworts than mosses germinated in the samples, especially those from lower altitudes. Samples from higher elevations produced twice the species diversity compared to those from lower elevations. They were able to identify the liverworts *Calypogeia arguta* (Figure 131), *C. fusca*, *Lepidozia wallichiana* (Figure 132), and *Zoopsis liukuensis* (Figure 133), all common taxa in the collection area. The diaspore origin of the liverworts could not be determined.



Figure 131. *Calypogeia arguta*, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Jan-Peter Frahm, with permission.

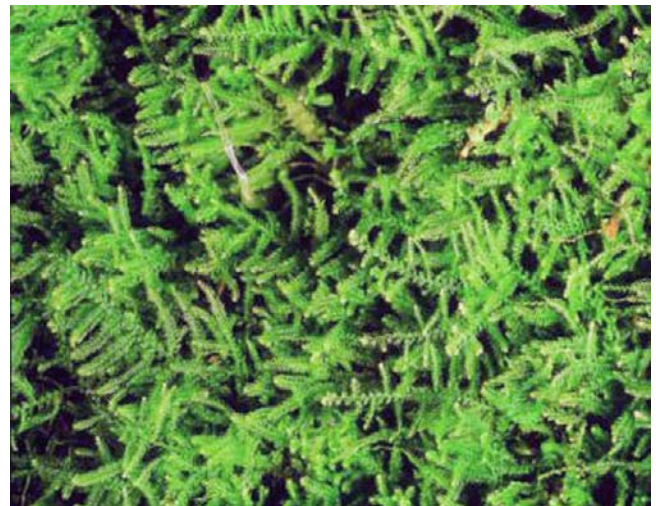


Figure 132. *Lepidozia wallichiana*, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Jia-dong Yang, through Creative Commons.



Figure 133. *Zoopsis liukuensis*, a species that survives in diaspore banks in Malaysian mountain rainforests. Photo by Rui-Liang Zhu, with permission.

Rheophilic Adaptations

River banks present problems unique to that habitat. The leafy liverwort *Cololejeunea stotleriana* (Figure 134) from Ecuador presents a highly specialized morphology and represents adaptations to that habitat (Figure 135) where little study has occurred (Gradstein *et al.* 2011). This species is both rheophilous and epiphyllous. Its adaptations include a robust stem, flatness, triangular lobules, large rhizoid fields not produced near each leaf base, super fertility, and clustered gynoeceia. It was growing with the rare mosses *Fissidens hydropogon* (Figure 136) and *Lepidopilum caviusculum* (Figure 137).



Figure 134. *Cololejeunea stotleriana* on a fern frond. Photo by F. Werner, courtesy of Robbert Gradstein.



Figure 135. Habitat of the rheophilous *Cololejeunea stotleriana*, *Fissidens hydropogon*, and *Lepidopilum caviusculum*. Photo by F. Werner, courtesy of Robbert Gradstein.



Figure 136. Herbarium specimen of *Fissidens hydropogon*, a rare rheophilic moss from Ecuador. Photo from Alchetron.com, through Creative Commons.



Figure 137. Herbarium specimen of *Lepidopilum caviusculum*, a rare rheophilic moss from Ecuador. Photo from the Natural History Museum, London, through Creative Commons.

Dispersal

Norhazrina *et al.* (2016) considered bryophytes to be very good dispersers, especially in contrast to flowering plants. This superior dispersal of bryophytes may lead to similar species richness patterns among the tropical regions, although tropical Africa has significantly fewer species than tropical America and tropical Asia. They found a slight but significantly higher beta diversity within tropical regions than among them. For many locations, oceans act as a barrier to "routine" dispersal, causing large-scale floristic patterns.

Suitable dispersal differs among regions and habitats. The tropics is in some places remote, separated from propagule sources by a wide expanse of ocean, and in others a mountain-valley topography likewise provides an expanse of unsuitable habitats. Thus, in discussing an area as expansive as the tropics, dispersal considerations are important for both biogeography and ecology.

With no experimental evidence but with vast ecological experience in the tropics and other regions, Richards (1988) ventured to apply his experience to hypothesize about dispersal of bryophytes in the tropics. First, he noted the impermanent nature of tropical substrates and suggested that these conditions would require efficient short-distance dispersal. He furthermore noted that each microhabitat has a distinct synusia of bryophytes that are characterized by particular life forms and life strategies. The swampy or oft-flooded sites are usually richer in species than sites that are well drained. The undergrowth probably has less effective wind dispersal than does the canopy.

For various asexual diaspores, splash is probably important (Richards 1988). For example, *Calymperopsis* species in Africa, as noted above, have their gemmae in splash cups. And discoid **Lejeuneaceae** (Figure 128-Figure 129) gemmae are probably dispersed by splashing rainfall. Richards also considered it likely that birds disperse fragments, particularly of **Meteoriaceae** (Figure 32-Figure 33), when they gather the mosses for nest building.

Baas-Becking (1934) introduced the concept that "everything is everywhere" for small things that can be dispersed by wind. The tropics seem like a good place to test this concept for bryophytes. Shaw *et al.* (2005) considered global patterns of moss diversity, patterns that must to some degree reflect dispersal patterns. Based on 86 globally distributed taxonomic checklists, they concluded that mosses are not more species-rich in the tropics than elsewhere. On the other hand, analysis of only North, Central, and South American samples demonstrate that a latitudinal gradient is apparent. Molecular diversity suggests that moss diversity is highest in the Southern Hemisphere, thus lowest in the Northern Hemisphere. The tropics are intermediate. These differences, however, are small, and essentially all moss lineages are represented in all three latitudinal zones. Hence, their data support the "everything is everywhere" hypothesis (Baas-Becking 1934) that is evident among many organisms with small propagules. (See Chapter 4-8 for more information on the topic of "everything is everywhere.")

But liverworts seem to exhibit a somewhat different pattern, more closely mimicking the distribution patterns of the tracheophytes (Schuster 1969). Schuster cites as evidence their patterns of endemism and disjunction, as well as their having highly specific, restricted ranges. He cites further support from the high number of species of liverworts in the Arctic. Nevertheless, some taxa, especially the **monoicous** (both sexes on same plant) ones, seem to have wide spore dispersal, as suggested by their

presence on islands in the Mid-Atlantic and Indian Ocean ridges. Interpretation is complicated by our inability to distinguish between ancient "overland" dispersal and more recent dispersal by spores.

But in 1969, tropical liverworts were poorly known. Can we still support Schuster's (1969) distributional conclusions today?

Based on analysis of a large, world-wide data set of species distributions, Wang *et al.* (2016) found a clearcut latitudinal diversity gradient in liverworts and hornworts. The highest species richness was found in the tropics, which they explained by the explosive diversification of some of the most speciose liverwort lineages, such as **Lejeuneaceae** (Figure 36-Figure 39, Figure 65, Figure 98-Figure 101, Figure 111-Figure 112, Figure 125-Figure 129, Figure 134), **Plagiochilaceae** (Figure 97), and **Frullaniaceae** (Figure 14, Figure 103) in the humid tropical forests. But they also noted that there is much evidence to suggest that dispersal is not limiting, and that long-distance dispersal is common among bryophytes. In fact, bryophytes exhibit a much lower global turnover of **beta diversity** (ratio between regional and local species diversity) than do flowering plants and maintain relatively constant levels of **alpha diversity** (local species richness) on a gradient of geographical isolation (Patiño *et al.* 2015).

New ideas are emerging suggesting that islands, including tropical islands, are sources of diversity instead of the previously thought evolutionary dead ends and diversity sinks (Patiño *et al.* 2015). The dead end concept was based on "perceived low levels of genetic diversity, poor interspecific competitive and defensive ability, and loss of dispersal capacities." But bryophytes do not fit well into this model. They have high dispersal capabilities compared to most tracheophytes, and when genetic diversity was examined, it proved to be higher in island populations than in continental populations. Patiño and coworkers suggest that rather than being evolutionary dead ends for such organisms as bryophytes, islands become sources of diversity for bryophytes that subsequently disperse to continents. They also found that species richness of islands correlates by habitat diversity, not by size or age of the islands or distance to the continent, hence is not driven by dispersal.

Karlin *et al.* (2012) examined genetic diversity on the remote Hawaiian Islands in the Neotropics. Because of this remoteness, the popular opinion was that long-distance dispersal to the islands was rare. In their investigation into the population genetic diversity, the researchers concluded that the peat moss *Sphagnum palustre* (Figure 138) most likely arrived with a single dispersal event. This species lacks sporophytes on the Hawaiian Islands and most likely lacks sexual reproduction. Further evidence to support a single dispersal event is that all samples share a rare genetic trait. They concluded that the original Hawaiian dispersal event was from vegetative propagation.



Figure 138. *Sphagnum palustre*, a species that apparently arrived on the Hawaiian Islands as a single dispersal event. Photo by Bernd Haynold, through Creative Commons.

Bryophytes exhibit a high capacity for transoceanic dispersal (Lewis *et al.* 2014) when compared to flowering plants (Patiño *et al.* 2014). This thinking is further supported by the low levels of competition among bryophytes compared to that among flowering plants (Rydin *et al.* 2009). This low competition suggests that the niche preemption hypothesis (Whittaker & Fernández-Palacios 2007) does not apply to bryophytes and thus makes it easier for them to succeed when they arrive on an island or subsequently on a new continent. The clonal nature of bryophytes (Cronberg *et al.* 2006; Hutsemékers *et al.* 2010, 2013; Karlin *et al.* 2011; Patiño *et al.* 2013), and their ability to disperse viable fragments means that the minimum population size is quite small (Bengtsson & Cronberg 2009) and further enables them to succeed when they colonize. Thus, as indicated by a compilation of data, island populations of bryophytes are not necessarily genetically depauperate (Fernández-Mazuecos & Vargas 2011; Laenen *et al.* 2011; Désamoré *et al.* 2012; García-Verdugo *et al.* 2015). Even seed plants can have a larger genetic diversity on islands than in associated continents (Désamoré *et al.* 2012). Based on these studies, and particularly that of Patiño *et al.* (2015), it is likely that the Macaronesian archipelagos, including the tropical portion, have provided a stepping stone for trans-continental bryophyte immigration to other tropical regions in new continental locations. Hence, islands may help to explain the **pantropical** (distribution covers tropical regions of both hemispheres) distribution of many bryophytes.

Another possibility, potentially as an additional scenario rather than a preferred one, is that islands can serve as refugia during times when the continent becomes uninhabitable. Such seems to be the case for the leafy liverwort *Radula lindenbergiana* (Figure 139) in Macaronesia (Laenen *et al.* 2011). It appears that a number of European plants, including *R. lindenbergiana*, share a Macaronesian common ancestor and that these species may have back-colonized Europe. The widespread (including tropical Africa and tropical America) aquatic moss *Platyhypnidium riparioides* (Figure 140-Figure 141) likewise supports the concept that oceanic islands serve as major sources of biodiversity for recolonization of continents following glaciation (Hutsemékers *et al.* 2013). The lack of morphological diversity among the bryophytes,

but presence of high genetic diversity, reflects the simple structure of the bryophytes.



Figure 139. *Radula lindenbergiana*, a species that seems to have used Macaronesia as a refugium. Photo by Dick Haaksma, with permission.



Figure 140. *Platyhypnidium riparioides* in its usual habitat. Photo by Hermann Schachner, through Creative Commons.

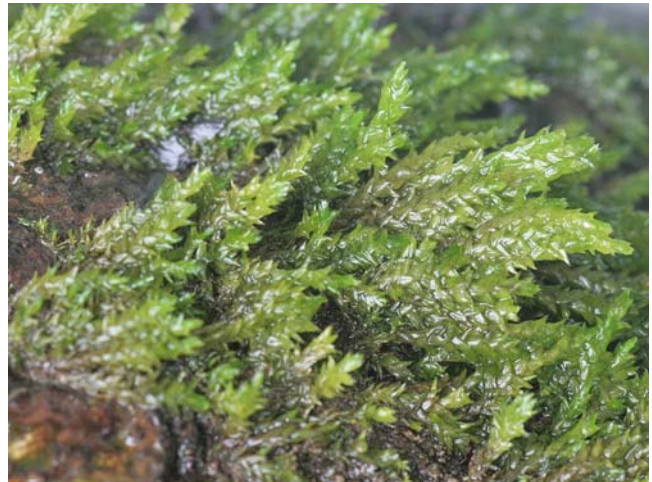


Figure 141. *Platyhypnidium riparioides*, a species that exhibits some genetic variation along its river course, using mostly fragments as dispersal units. Photo by Hermann Schachner, through Creative Commons.

For the moss *Platyhypnidium riparioides* (Figure 140-Figure 141), Hutsemékers *et al.* (2013) found that some genetic variation occurs along the river basin and indicates that this widespread aquatic moss has weaker dispersal than

that expected for pollen or wind-dispersed seeds. Rather, it appears that fragments are more important than spores for local dispersal of this moss, thus explaining the low levels of genetic diversity.

Even the dispersal-limited dung moss *Tetraplodon* (Figure 142) has **amphitropical** (distributed on both sides of the tropics) and bipolar (distributed in cold temperate regions) disjunctions that seem to require long-distance dispersal (Lewis *et al.* 2014). Lewis and coworkers suggested that the disjunct distribution in the Western Hemisphere may have been accomplished through stepwise migration along the Neotropical Andes. But *Tetraplodon* is typically dispersed by flies that provide only short dispersal ranges. Furthermore, experiments indicate that the spores of *Tetraplodon* cannot survive long-distance dispersal by wind. The researchers suggest that instead, birds might provide the dispersal vector necessary to account for the widespread but disjunctive distribution of the species in South America.



Figure 142. *Tetraplodon mniioides*, an amphitropic moss, with the toad *Nannophryne variegata* in South America. Photo by Filipe Osorio, with permission.

In examining bryophytes on oceanic islands, Patiño *et al.* (2013) concluded that even bryophytes exhibit an island syndrome. They exhibit genetic drift, indicating relatively slow migration rates between the oceanic islands and continents. This suggests that the ocean does impede migration. This period of isolation seems to lead to an increase in production of specialized asexual diaspores and a decrease in sporophyte production on the oceanic islands.

To demonstrate the relatively large number of Afro-American distributions in bryophytes, Gradstein (2013) examined records of liverworts in tropical regions of both Old World and New World tropics. Based on the disjunctions of 74 liverworts in 13 genera with Afro-American ranges, he estimated that about 5% of the Neotropical and 8% of the African liverwort species had Afro-American disjunct distributions. This number is

doubled when pantropical species are included. Gradstein cited spore dispersal experiments and molecular-phylogenetic studies to conclude that for the majority of these genera, long-distance dispersal was the reason for the disjunction.

Ah-Peng *et al.* (2010) demonstrated the high bryophyte diversity on the small, oceanic La Reunion Island. In only 2512 km², 776 taxa are known. This island is near East Africa and Madagascar. The high diversity is fostered by its subtropical climate, a high altitudinal range (to 3070 m asl), and high rainfall.

Much of our understanding of long-range dispersal comes from van Zanten (1978; van Zanten & Pócs 1981; van Zanten and Gradstein 1987). In their laboratory experiments using 86 Colombian liverwort species, van Zanten & Gradstein (1987) found that spores of transoceanic species were more durable than those of endemic species. Survival was also greater in wet air-currents at high altitudes than in dry air currents. When they placed the spores on airplane wing tips during flights at jetstream elevation from Amsterdam to Los Angeles and back, however, only two species, the endemic *Marchantia chenopoda* (Figure 143) and the transoceanic *Gymnocoleopsis cylindriciformis*, could survive. All others were dead, probably due to exposure to UV radiation. Presumably *G. multiflora* spores survive because this species grows in the high Andes above 4000 m, where UV radiation is high. Van Zanten and Pócs (1981) concluded that tropical lowland moss species are much less drought tolerant than are temperate species. These tropical species are, however, resistant to wet-freezing and can be dispersed over short distances by rain showers and typhoons. They concluded that north-south dispersal across the equator was the most difficult and occurred rarely, if at all.



Figure 143. *Marchantia chenopoda* archegoniophores, a species whose spores can survive flight on the wings of a jet plane. Photo by Janice Glime.

Dispersal by wind is considered limited in forests, except in the canopy (Richards 1988). Some species, such as African moss species of *Syrrhopodon* (Figure 144) subsect. *Calymperopsis*, produce gemmae in splash cups similar to those of the moss *Tetraphis pellucida* (Figure 145). Although experimental dispersal studies are lacking for tropical species, but Richards suggests that the discoid gemmae (Figure 126) of many of the *Lejeuneaceae* (Figure 128-Figure 129) are probably dispersed by

splashing rain. Hanging mosses get dispersed by birds through dropped fragments when they are collected for nest making.



Figure 144. *Syrrhopodon albobaginatatus*; some species of this genus produce gemmae in cups in the tropics. Photo from Natural History Museum, London, through Creative Commons.



Figure 145. *Tetraphis pellucida* with gemmae cup and discoid gemmae – similar to those of African species of *Syrrhopodon*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Dispersal adaptations reflect moisture relationships. The secretion of sticky mucilage (Thiers 1988) can aid in the attachment to vertical surfaces and prevent being washed away during rainstorms. Gemmae and the precocious development of spores permit more rapid development and thus greater chance for establishment. The prolongation of the protonemal stage may also aid in insuring attachment, whereas the **neotenus life cycle** (see under Liverworts above) permits early maturity, providing greater likelihood of completion of the life cycle before host leaves are shed during the rainy season.

I must re-emphasize the strategies of the **Lejeuneaceae** (Figure 36-Figure 39, Figure 128-Figure 129), a large pantropical family of considerable importance among the liverworts. This family has many monoicous species, and many species have intercontinental ranges, but all have large, multicellular spores – an atypical character for taxa with transoceanic distributions (Gradstein *et al.*

1983; Gradstein & Pócs 1989). Nevertheless, the multicellular large spores should permit the species to become established more easily once they arrive because of greater food reserves to permit a quick start. And the monoicous character facilitates sexual reproduction.

Sampling

Sampling in the tropics can present problems that are less important elsewhere – such difficulties as canopy height and excessive moisture. Mountainous areas may be remote, with some available only by foot paths. Tall trees make small branches of the canopy almost impossible to sample; methods to overcome this obstacle are in the subchapter on epiphytes. Several researchers have addressed the problems unique to bryological collecting in the tropics (Mori & Holm-Nielsen 1981; Edwards 1986; Delgadillo 1987; O'Shea 1989; see Frahm *et al.* 2003 for a comprehensive review).

One important consideration when collecting in tropical countries is that researchers there are often struggling with inadequate herbarium materials, particularly ones that can be used for checking their own collections. Duplicate specimens should always be provided to an accessible herbarium in the country – one that has a curator and can loan specimens. And of course one should be aware of local collection laws, obtain proper collecting permits, and determine in advance what restrictions there might be by customs and plant control in both the country of collection and in the receiving country.

Delgadillo (1987) and Frahm *et al.* (2003) detail many things to consider before departing for the tropical country, behavior during the visit, and how to treat specimens from another country upon return home. He suggests researching the geography, customs, and language of the country and contacting one or more resident bryologists for suggestions on places to stay and places to sample. Obtain collecting permits in advance for each country you plan to visit. Be sure you have health insurance to cover you in the places you will visit. Follow the routines of the local herbaria and institutions you visit and take their advice on food, roads, and other items of local knowledge. Remember that appointment times are not as rigid in some countries, so be patient, especially with local natives who might help you. Be sure you provide the local herbaria or national herbarium with a set of identified specimens. If possible, use their herbarium specimens in their herbarium so you don't have to borrow from their typically small number of specimens. To get both loans and your own specimens back to your own country, use registered mail. Be sure you understand the quarantine regulations in both countries. Avoid travelling in the field alone; taking a local student along can benefit both of you. Carry a first-aid kit and a letter of introduction from the local university or herbarium in case it is needed to satisfy local authorities. Upon returning home, return loaned specimens as soon as possible, being sure to meet quarantine requirements. Send a set of duplicate specimens from your own identified collections for any species you have not already deposited in a herbarium in the country visited.

Braun-Blanquet Sampling Method

While sampling may be more difficult in a tropical jungle, methods used elsewhere often work well. A

common method of sampling vegetation, particularly in Europe, is the Braun-Blanquet method. This method uses a cover-abundance scale to describe the vegetation. These levels are divided into cover classes, typically using 5-7 categories:

1	<1
2	1-5
3	5-10
4	10-25
5	25-50
6	50-75
7	75-100

The levels are estimated through the use of relevés. This system has been applied originally to tracheophytes, but many bryologists have adapted it for a more efficient means of quantitative sampling. Poore (1955) criticized the system, but Moore (1962) countered those criticisms, stating that Poore had misapplied the method. Damgaard (2014) determined that despite its bias to over-estimate abundance, the Braun-Blanquet method gave results comparable to those of other methods of estimating plant cover. It has the added advantage of providing comparisons to the many studies that have used it, permitting data comparisons over time.

Wikum and Shanholtzer (1978) noted that most methods of measuring vegetation density are time-consuming and costly. The Braun-Blanquet method requires only about one-third to one-fifth the amount of field time, giving comparable results. I am unaware of any studies comparing the Braun-Blanquet system with other cover estimates for bryophytes, but it has been used in tropical studies and provides a relatively rapid method that is helpful when time is often quite limited.

A discussion of the unique methods for sampling epiphytes is in the subchapters on epiphytes and epiphylls in this chapter.

Drying Specimens

Because of periods of daily rain, there isn't enough time for anything to get dry, and that includes your clothes and your bryophytes. And both damp clothing and bryophytes can soon become a garden for molds. Molds make the bryophytes difficult to identify, and certainly make them unsightly, not to mention a health hazard. They introduce molds to the herbarium, and their spores can cause allergic reactions and asthma. They will also make it more difficult to get the bryophytes through plant protection agencies when you enter another country. Frahm and Gradstein (1986) note these difficulties in the tropics, making several suggestions to overcome them.

One method that is used is to place the bryophytes in paper bags on a dry floor of a tent with open flaps (Frahm & Gradstein 1986). The opening is covered with mosquito netting to permit air movement. But during the rainy season, the dry periods are often insufficient for the bryophytes to dry. Some bryologists have resorted to putting a professional plant dryer in the back of a truck, using butane to provide the heat. But this method is not practical when only foot paths are available to the campsite. And most budgets can't afford such equipment. A less expensive approach is to suspend the bryophytes near a campfire, but the fire might get too hot and thus

requires close watching. It can heat the bryophytes too much and thus damage them, particularly for those who might later want to use them for chemical analysis.

Frahm and Gradstein (1986) suggest an inexpensive, lightweight apparatus for drying bryophytes (Figure 146). It is constructed of L-shaped aluminum pieces with a frame that supports a wire mesh. Nylon should not be used because of its flammability. The heat source is two kerosene camping stoves (see also Croat 1979). The structure should then be surrounded with cotton cloth, as shown in the inset, again avoiding the more flammable nylon. The frames are about 1 m high, but the level of the screen can be adjusted to change the heat level. The apparatus should be monitored until you learn how much flame you need to avoid toasting the bryophytes or causing a forest fire. Once the ideal flame size is determined, the apparatus can be left unguarded overnight.

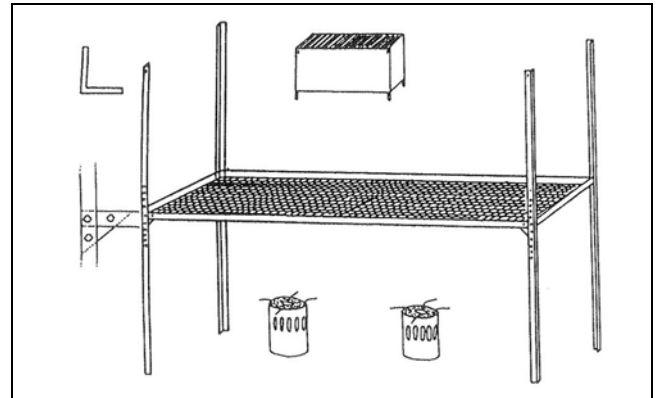


Figure 146. Light-weight drying apparatus for bryophytes in the field. From Frahm & Gradstein 1986.

Greene (1986) used chicken wire instead of wire screening. He suggested a method for keeping the specimens dry once getting them that way. They should immediately be put into large, heavy-duty plastic bags with silica gel to absorb moisture and sealed. [The plastic bags can be sealed by folding in the top corners, then folding down the top several times and fastening it with several large paper clips. – JG.] The specimens themselves can be kept in paper bags or packets. Greene transported the silica gel containers to the site in cotton bags. When they were needed, the silica gel containers were put into paper specimen bags and heated along with the specimens so that they were dry and ready when the specimens were stored.

Summary

Bryophytes in the tropics undoubtedly have a crucial role in water and nutrient retention, releasing nutrients during re-wetting, but filtering them from the lower branches and ground during rain events. Because of their sponge-like behavior, they can maintain moisture and nutrients for other members of the ecosystem. Nutrients can be released slowly, providing nutrients to the forest floor at critical times.

The primary environmental drivers determining the types of bryophyte communities are moisture, temperature, and light intensity. Life and growth forms differ among the habitats, with such forms as **pendants**,

fans, and **tails** in moist habitats and **mats** and short acrocarpous mosses in dry conditions. Likewise, productivity differs with habitat, with dense growths in wet cloud forests and little biomass on the rainforest floor where there is little light penetration. Furthermore, growth periods and reproduction coincide with rainy periods, whereas the bryophytes are typically dormant in dry seasons.

Moss reproduction varies with habitat, but antheridia and archegonia are typically produced during the rainy season. **Monoicous** species have the most sexual reproduction. Many species lack sexual reproduction and spread through gemmae and regrowth. Sun species typically have larger spores than do shade species. Protonemal development is often prolonged.

Some liverworts and a few mosses may exhibit **neoteny**. Liverworts often have shortened life cycles, fewer antheridia and archegonia, longer spore lives, longer protonemal stages, and few types of gemmae in the tropics. Both mosses and liverworts can survive as spores, vegetative propagules, or fragments in diaspore banks, but liverwort spores typically have short longevity in the tropics. Liverworts have a limited number of propagule types, whereas the mosses have many.

Dispersal is mostly by wind and occurs in most cases in the dry season. Long distance dispersal is often important between mountains, and some species exhibit disjunct distributions between Africa and the Neotropics.

Rheophilic species probably have similar adaptations to the stream habitat, but few tropical studies have occurred.

Sampling brings special problems of getting mosses dry in the cloud forest or in the rainy season, often necessitating drying racks and a heat source. Investigators need to gain permission and should leave a set of herbarium specimens with a notable herbarium in the host country.

Diversity, endemicity and conservation. *Cryptog. Bryol.* 31: 241-270.

Akande, A. O. 1984. Anhydrobiosis in corticolous bryophytes. *Trop. Ecol.* 25: 255-259.

Akande, A. O. 1985. Osmotic potential – A factor for resistance to water stress in some Nigerian species of corticolous bryophytes. *Trop. Ecol.* 26: 80-84

Alfayate, C., Ron, E., Estébanez, B., and Pérez-Batista, M. Á. 2013. Mature spores of four pleurocarpous mosses in the Canary Islands: Ultrastructure and early germination stages. *Bryologist* 116: 97-112.

Baas Becking, L. G. M. 1934. Geobiologie of inleiding tot de milieukunde. W. P. Van Stockum & Zoon, The Hague, The Netherlands.

Barkman, J. J. 1958. Phytosociology and Ecology of Cryptogamic Epiphytes. van Gorcum, Assen, 628 pp.

Batista, W. V. S. M., Pôrto, K. C., and Santos, N. D. 2018. Distribution, ecology, and reproduction of bryophytes in a humid enclave in the semiarid region of northeastern Brazil. *Acta Bot. Brasil.* 32: 303-313.

Bengtsson, B. O. and Cronberg, N. 2009. The effective size of bryophyte populations. *J. Theor. Biol.* 258: 121-126.

Biebl, R. 1964. Temperaturreistenz tropischer Pflanzen auf Puerto Rico. [Temperature resistance of tropical plants in Puerto Rico.]. *Protoplasma* 59: 133-156.

Biebel, R. 1967. Temperaturreistenz tropischer Urwaldmoose. [Temperature resistance of tropical jungle moss.]. *Flora* 157: 25-30.

Bisang, I., Piippo, S., and Hedenäs, L. 2003. Bryophyte diaspore bank in three Malaysian mountain rainforests. *J. Bryol.* 25: 68-70.

Bryant, E. H., Crandall-Stotler, B., and Stotler, R. E. 1973. A factor analysis of the distribution of some Puerto Rican liverworts. *Can. J. Bot.* 51: 1545-1554.

Cardoso, A. W. 2012. Bryophytes in the hydrological cycle and climate change implications: A case study of La Réunion cloud forest. Ph. D. dissertation, University of Cape Town, S. Afr.

Cerqueira, G. R., Ilkiu-Borges, A. L., and Ferreira, L. V. 2016. Seasonality of reproduction of epiphytic bryophytes in flooded forests from the Caxiuanã National Forest, Eastern Amazon. *An. Acad. Brasil. Ciên.* 88: 903-910.

Chen, X., Liu, W. Y., Song, L., Li, S., Wu, C. S., and Lu, H. Z. 2016. Adaptation of epiphytic bryophytes in the understory attributing to the correlations and trade-offs between functional traits. *J. Bryol.* 38: 110-117.

Churchill, S. P., Sanjines A., N. N., and Aldana M., C. 2010. Catálogo de las briofitas de Bolivia: Diversidad, distribución y ecología. Missouri Botanical Garden, 340 pp.

Coley, P. D., Kursar, T. A., and Machado, J.-L. 1993. Colonization of tropical rain forest leaves by epiphylls: Effects of site and host plant leaf lifetime. *Ecology* 74: 619-623.

Cornelissen, J. H. C. and Steege, H. ter. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.

Coxson, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Can. J. Bot.* 69: 2122-2129.

Coxson, D. S., McIntyre, D. D., and Vogel, H. J. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). *Biotropica* 24: 121-133.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make an early version of this chapter reliable. Her helpful discussions kept me going on this part of the world I know so little about. My co-author, Robbert Gradstein, has been very helpful in discussions, obtaining images and references, and in providing a critical review of the chapter. Without his input this chapter would be far less complete. Tatiany Oliveira da Silva provided a critical reading for clarity, provided additional references, and shared her knowledge of the Amazon.

Literature Cited

Acebey, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.

Ah-Peng, C., Bardat, J., Stamenoff, P., Hedderson, T. A., and Strasberg, D. 2010. Bryophytes of the island of La Réunion:

- Croat, T. B. 1979. Use of a portable propane gas oven for field drying plants. *Taxon* 28: 573-580.
- Cronberg, N., Rydgren, K., and Økland, R. H. 2006. Clonal structure and genet-level sex ratios suggest different roles of vegetative and sexual reproduction in the clonal moss *Hylocomium splendens*. *Ecography* 29: 95-103.
- Damgaard, C. 2014. Estimating mean plant cover from different types of cover data: A coherent statistical framework. *Ecosphere* 5(2): 1-7.
- Datta Munshi, J. 1974. Seasonal changes in standing crop and annual net production of two moss communities at Varanasi. *Trop. Ecol.* 15: 28-38.
- Delgadillo M., C. 1976. Estudio botánico y ecológico de la región de Río Uxpanapa, Veracruz. No. 3. Los Musgos. Publ. Inst. Invest. Recurs. Bioticos 1: 19-28.
- Delgadillo M., C. 1987. Additional recommendations for bryologists visiting the tropics. *Taxon* 36: 289-291.
- Delgadillo M., C. 1993. The Neotropical-African disjunction. *Bryologist* 96: 604-615.
- Désamoris, A., Laenen, B., Carine, M. A., Gonzalez-Mancebo, J. M., Molina, R. J., and Vanderpoorten, A. 2012. Inverted patterns of genetic diversity in continental and island populations of the heather *Erica scoparia* s.l. *J. Biogeogr.* 39: 574-584.
- During, H. J. 1998. De diasporenvoorraad in de bodem van een savanne in Zimbabwe. [The diaspore bank in the bottom of a savannah in Zimbabwe.]. *Bauxbaumiella* 45: 12-13.
- During, H. J. 2007. Episodic bryophytes in the diaspore bank of a Zimbabwean savanna. *Lindbergia* 32: 55-61.
- During, H. J. and Moyo, C. 1999. The diaspore bank of bryophytes in a Zimbabwean savanna. *Hausknechtia Beiheft (Riclef Grolle-Festschrift)* 9: 111-114.
- Edwards, S. R. 1986. Bryophyte collecting and plant photography. *Univ. Hull Dept. Geogr. Misc. Ser.* 30: 65-72; 102-108.
- Egunyomi, A. 1978. The distribution of pantropical moss, *Octoblepharum albidum* Hedw. in Africa with special reference to Nigeria. *Rev. Bryol. Lichénol.* 44: 141-148.
- Egunyomi, A. 1979a. Autecology of *Octoblepharum albidum* Hedw. in Western Nigeria II. Phenology and water relations. *Nova Hedw.* 31: 377-389.
- Egunyomi, A. 1979b. The viability of spores of some tropical moss species after long-time storage and their survival changes in nature. *J. Hattori Bot. Lab.* 45: 167-171.
- Egunyomi, A. 1982. Dispersal mechanisms of *Bryum coronatum* in Nigeria. *Lindbergia* 8: 89-92.
- Egunyomi, A. 1984. A survey of asexual reproductive diaspores in the Nigerian moss flora. *J. Hattori Bot. Lab.* 56: 115-121.
- Egunyomi, A., Harrington, H. J., and Olarinmoye, S. O. 1980. Studies on regeneration from the leaves of *O. albidum* Hedw. (Musci). *Cryptog. Bryol. Lichénol.* 1: 73-84.
- Fatoba, P. O. 1998. Reproductive phenology of three selected tropical African mosses in South Western Nigeria. *Niger. J. Bot.* 11: 25-33.
- Fernández-Mazuecos, M. and Vargas, P. 2011. Genetically depauperate in the continent but rich in oceanic islands: *Cistus monspeliensis* (Cistaceae) in the Canary Islands. *PLoS One* 6: e17172.
- Fleischer M. 1904-1923. Die Musci der Flora von Buitenzorg (zugleich Laubmoosflora von Java), 5 vols. Brill, Leiden.
- Frahm, J.-P. 1990a. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedw.* 51: 151-164.
- Frahm, J.-P. 1990b. Bryophyte phytomass in tropical ecosystems. *Bot. J. Linnean Soc.* 104: 22-33.
- Frahm, J.-P. and Gradstein, S. R. 1986. An apparatus for drying bryophytes in the field. *Bryol. Times* 38: 5.
- Frahm, J.-P. and Gradstein, S. R. 1990. Ecology of tropical bryophytes: A bibliography. *Trop. Bryol.* 3: 75-77.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Frahm, J.-P. and Kürschner, H. 1992. Moose tropischer Regenwälder. [Moss of tropical rainforests.]. *Spektr. Wissen.* 10: 58-67.
- Frahm, J.-P., Pócs, T., O'shea, B., Koponen, T., Piipo, S., Enroth, J., Rao, P., and Fang, Y. 2003. Manual of Tropical Bryology. *Trop. Bryol.* 23: 1-196.
- Frangi, J. L. and Lugo, A. E. 1992. Biomass and nutrient accumulation in ten year old bryophyte communities inside a flood plain in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 24: 106-112.
- Frey, W., Gossow, R., and Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserleitenden und wasserspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord-Borneo). *Nova Hedw.* 51(1-2): 87-119.
- Fulford, M., Crandall, B., and Stotler, R. 1970. The ecology of an elfin forest in Puerto Rico, 11. The leafy Hepaticae of Pico del Oeste. *J. Arnold Arbor.* 51: 56-69.
- Fulford, M., Crandall, B., and Stotler, R. 1971. The ecology of an elfin forest in Puerto Rico. Part 15. A study of the leafy hepatic flora of the Luquillo Mountains. *J. Arnold Arbor.* 52: 435-458.
- García-Verdugo, C., Sajeva, M., Mantia, T. La, Harrouni, C., Msanda, F., and Caujapé-Castells, J. 2015. Do island plant populations really have lower genetic variation than mainland populations? Effects of selection and distribution range on genetic diversity estimates. *Molec. Ecol.* 24: 726-741.
- Gehrig-Downie, C., Obregón, A., Bendix, J., and Gradstein, S. R. 2011. Epiphyte biomass and canopy microclimate in the tropical lowland cloud forest of French Guiana. *Biotropica* 43: 591-596.
- Gehrig-Downie, C., Obregón, A., Bendix, J., and Gradstein, S. R. 2013. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *J. Bryol.* 35: 243-254.
- Giesenhagen, K. 1910. Die Moostypen de Regenwälder. [The moss types of rainforests.]. *Ann. Jard. Bot. Buitenz.* (suppl. 3, pt.2): 711-790.
- Goebel, K. 1888. Morphologische und biologische Studien. I. Über epiphytische Farne und Muscineen. *Ann. Jard. Bot. Buitenzorg* 7: 1-73.
- Gradstein, S. R. 1975. Studies on Lejeuneaceae subfam. Ptychanthoideae III. A taxonomic monograph of the genus *Acrolejeunea* (Hepaticae). *Bryophyt. Biblioth.* 4: 1-162.
- Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. *Cryptog. Bryol.* 27: 141-152.
- Gradstein, S. R. 2013. Afro-American hepatics revisited. *Polish Bot. J.* 58: 149-177.
- Gradstein S. R. and Benitez, A. 2014. A second locality for the critically endangered *Colura irrorata* (Lejeuneaceae) in the Ecuadorian Andes. *J. Bryol.* 36: 151-155.
- Gradstein, S. R. and Ilkiu-Borges, A. L. 2009. Guide to the Plants of Central French Guiana. Part 4. Liverworts and Hornworts. *Mem. N. Y. Bot. Gard.* 76(4): 140 pp.

- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies. Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R. and Wilson, R. 2009. Protonemal neoteny in bryophytes. In: Mohamed, H., Baki, B. B., Nasrullah-Boyce, A., and Lee, P. K. Y. (eds.). Bryology in the New Millennium. University of Malaya, Kuala Lumpur, pp. 1-11.
- Gradstein, S. R., Pócs, T., and Vána, J. 1983. Disjunct Hepaticae in tropical America and Africa. *Acta Bot. Hung.* 29: 127-171.
- Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001. Guide to the Bryophytes of Tropical America. *Mem. N. Y. Bot. Gard.* 86: 1-577.
- Gradstein, S. R., Reiner-Drehwald, M. E., and Jost, L. 2004. The systematic position and distribution of *Myriocolea irrorata* (Lejeuneaceae, Hepaticae), an endangered liverwort from the Ecuadorian Andes. *J. Hattori Bot. Lab.* 93: 235-248.
- Gradstein, S. R., Wilson, R., Ilkiu-Borges, A. L., and Heinrichs, J. 2006. Phylogenetic relationships and neotenic evolution of *Metzgeriopsis* (Lejeuneaceae) based on chloroplast DNA sequences and morphology. *Bot. J. Linn. Soc.* 151: 293-308.
- Gradstein, S. R., Ilkiu-Borges, A. L., and Vanderpoorten, A. 2011. Habitat specialization triggers the evolution of unusual morphologies – the case of *Cololejeunea stotleriana* sp. nov. from Ecuador. *Bryologist* 114: 9-22.
- Greene, S. W. 1986. Keeping them dry. *Bryol. Times* 38: 6.
- Greenwood, J. L. and Stark, L. R. 2014. The rate of drying determines the extent of desiccation tolerance in *Physcomitrella patens*. *Funct. Plant Biol.* 41: 460-467.
- Griffin, D. III. 1979. Briofitos y Liqueños de los paramos. pp. 79-87. In: Salgado-Labrador, M. L. (ed.). El Medio Ambiente Paramo. Mérida, Venezuela. Centro de Estudios Avanzados, Ediciones CEA-IVIC, Caracas.
- Griffin, D. III, Breil, D. A., Morales-Zürcher, M. I., and Eakin, D. 1974. Observations on bryophyte community of the Poas Volcano, Costa Rica. Observaciones sobre la comunidad de Briófitas del Volcán Poás, Costa Rica. *Misc. Bryol. Lichenol.* 6: 174-175.
- Hofstede, R. G. M., Wolf, J. H. D., and Benzig, D. H. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forests. *Selbyana* 14: 37-45.
- Hosokawa, T., Odani, N., and Tagawa, H. 1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. *Bryologist* 67: 396-411.
- Hutsemékers, V., Hardy, O. J., Mardulyn, P., Shaw, A. J., and Vanderpoorten, A. 2010. Macroecological patterns of genetic structure and diversity in the aquatic moss *Platyhypnidium riparioides*. *New Phytol.* 185: 852-864.
- Hutsemékers, V., Szövényi, P., Shaw, A. J., González-Mancebo, J. M., Muñoz, J., and Vanderpoorten, A. 2011. Oceanic islands are not sinks of biodiversity in spore-producing plants. *Proc. Natl. Acad. Sci.* 108: 18989-18994.
- Hutsemékers, V., Hardy, O. J., and Vanderpoorten, A. 2013. Does water facilitate gene flow in spore-producing plants? Insights from the fine-scale genetic structure of the aquatic moss *Rhynchostegium riparioides* (Brachytheciaceae). *Aquat. Bot.* 108: 1-6.
- Ingram, S. W. and Nadkarni, N. M. 1993. Composition and distribution of epiphytic organic matter in a Neotropical cloud forest, Costa Rica. *Biotropica* 25:370-383.
- Jácome, J., Gradstein, S. R., and Kessler, M. 2011. Response of epiphytic bryophyte communities to simulated climate change in the Tropics. In: Tuba, Z., Slack, N., and Stark, L. (eds.). Bryophyte Ecology and Climate Change. Cambridge University Press, pp. 191-210.
- Johnson, A., and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. *Bryologist* 73: 682-686.
- Karger, D. N., Kluge, J., Abrahamczyk, S., Salazar, L., Homeier, J., Lehnert, M., Amoroso, V. B., and Kessler, M. 2012. Bryophyte cover of trees as proxy for air humidity in the tropics. *Ecol. Indic.* 20: 277-281.
- Karlin, E. F., Andrus, R. E., and Shaw, A. J. 2011. One haploid parent contributes 100% of the gene pool for a wide spread species in northwest North America. *Molec. Ecol.* 20: 753-767.
- Karlin, E. F., Hotchkiss, S. C., Boles, S. B., Stenoien, H. K., Hassel, K., Flatberg, K. I., and Shaw, A. J. 2012. High genetic diversity in a remote island population system: *Sans sex*. *New Phytol.* 193: 1088-1097.
- Krinsky, N. I. 1968. The protective function of carotenoid pigments. *Photophysiology: Current Topics* 3: 123-195.
- Kürschner, H. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. *Turkish J. Bot.* 28: 73-84.
- Kürschner, H. and Parolly, G. 1998a. Lebensstrategien stammepiphytischer moose in regenwaldern am andenostabhang und im Amazonas-Tiefland von nord-Peru. [Life strategies of epiphytic bryophyte vegetation in rainforests along the eastern Andean slopes and the Amazon lowlands of northern Peru]. *Nova Hedw.* 67: 1-22.
- Kürschner, H. and Parolly, G. 1998b. Lebensformen und adaptationen zur wasserleitung und wasserspeicherung in epiphytischen moosgesellschaften nord-Perus (Amazonas-tiefland, cordillera oriental, cordillera central). [Life forms and adaptations to water conduction and water storing in epiphytic bryophyte communities in northern Peru (the Amazon lowlands, eastern and central cordillera).]. *Nova Hedw.* 67: 349-379.
- Kürschner, H., Frey, W., and Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – A pantropical synopsis. *Nova Hedw.* 69: 73-99.
- Laenen, B., Désambré, A., Devos, N., Shaw, A. J., González-Mancebo, J. M., Carine, M. A., and Vanderpoorten, A. 2011. Macaronesia: A source of hidden genetic diversity for post – glacial recolonization of western Europe in the leafy liverwort *Radula lindenbergiana*. *J. Biogeogr.* 38: 631-639.
- Larson, D. W. 1981. Differential wetting in some lichens and mosses: The role of morphology. *Bryologist* 84: 1-15.
- Lawton, R. and Dryer, V. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18: 101-116.
- Lewis, L. R., Rozzi, R., and Goffinet, B. 2014. Direct long-distance dispersal shapes a New World amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon* (Bryopsida: Splachnaceae). *J. Biogeogr.* 41: 2385-2395.
- Li, X., Glime, J. M., and Hattori, S. 1989. Ecological gradient analysis of the genus *Frullania* on Mt. Albert Edward, Papua New Guinea. *J. Hattori Bot. Lab.* 66: 359-369.
- Linares, E. L. 1986. Estudio taxonomico y ecologico de la brioflora en la franja alto andina de "El Tabalzo", Cundinamarca. [Taxonomic and ecological study of the bryoflora in the high Andean strip of "El Tabalzo," Cundinamarca.]. Ph.D. Thesis, Universidad Nacional de Colombia, Bogotá, 308 pp.
- Lisboa, R. C. L. 1976. Estudos sobre a vegetação das campinas amazonicas V. Briocologia de uma campina amazonica. *Acta Amazon.* [Studies on the vegetation of the Amazonian

- plains V. Bryoecology of an Amazonian plain. *Acta Amazon.* 6: 171-191.
- Lösch, R., Mülders, P., Fischer, E., and Frahm, J.-P. 1994. Photosynthetic gas exchange of bryophytes from tropical lowland and mountain forests of eastern Central Africa. *Trop. Bryol.* 9: 169-186.
- Maciel-Silva, A. S. and Oliveira, M. P. 2016. How tropical moss sporophytes respond to seasonality: Examples from a semi-deciduous ecosystem in Brazil. *Cryptog. Bryol.* 37: 227-239.
- Maciel-Silva, A. S. and Valio, I. F. M. 2011. Reproductive phenology of bryophytes in tropical rain forests: The sexes never sleep. *Bryologist* 114: 708-719.
- Maciel-Silva, A. S., Valio, I. F. M., and Rydin, H. 2012a. Altitude affects the reproductive performance in monoicous and dioicous bryophytes: Examples from a Brazilian Atlantic rainforest. *AoB Plants* 2012, pls016,14 pp.
- Maciel-Silva, A. S., Valio, I. F. M., and Rydin, H. 2012b. Diaspore bank of bryophytes in tropical rain forests: The importance of breeding system, phylum and microhabitat. *Oecologia* 168: 321-333.
- Maciel-Silva, A. S., Coelho, M. L. P., and Pôrto, K. C. 2013. Reproductive traits in the tropical moss *Octoblepharum albidum* Hedw. differ between rainforest and coastal sites. *J. Bryol.* 35: 206-215.
- Mägdefrau, K. 1982. Life-forms in bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 45-58.
- Makinde, A. M. and Odu, E. A. 1994. Phenological studies of selected savanna mosses of south-western Nigeria. *Experientia* 50: 616-619.
- Merwin, M. C. and Nadkarni, N. M. 2002. 100 years of tropical bryophyte and lichen ecology: A bibliographic guide to the literature from 1901-2000. *Trop. Bryol.* 21: 47-67.
- Miehe, G. and Miehe, S. 1994. East African bryophytes. XII. Bryophytes from Bale Mountains, SE Ethiopia. 1. Phytoecological introduction. *Fragm. Flor. Geobot.* 39: 165-219.
- Mishler, B. D. 1988. Reproductive ecology of bryophytes. In: Lovett Doust, J. and Lovett Doust, L. *Plant Reproductive Ecology: Patterns and Strategies*. Oxford University Press, Oxford, pp. 285-306.
- Mitten, W. 1869. Musci Austro-Americani. *J. Linn. Soc. Bot.* 12: 1-659.
- Monge-Nájera, J. 1989. The relationship of epiphyllous liverworts with leaf characteristics and light in Monte Verde, Costa Rica. *Cryptog. Bryol. Lichénol.* 10: 345-352.
- Moore, J. J. 1962. The Braun-Blanquet System: A reassessment. *J. Ecol.* 50: 761-769.
- Moreno, E. J. 1992. Revisión histórica de la briología en Venezuela. *Trop. Bryol.* 6: 139-146.
- Mori, S. A. and Holm-Nielsen, L. B. 1981. Recommendations for botanists visiting Neotropical countries. *Taxon* 30: 87-89.
- Nadkarni, N. M. 1984. Epiphyte biomass and nutrient capital of a Neotropical elfin forest. *Biotropica* 16: 249-256.
- Nadkarni, N. M., Cobb, A. R., and Solano, R. 2000. Interception and retention of macroscopic bryophyte fragments by branch substrates in a tropical cloud forest: An experimental and demographic approach. *Oecologia* 122: 60-65.
- Nasrulhaq-Boyce, A., Haji Mohamed, M. A., Lim, A. L., Barakbah, S. S., Yong, K. T., and Nor, D. M. 2011. Comparative morphological and photosynthetic studies on three Malaysian species of *Pogonatum* from habitats of varying light irradiances. *J. Bryol.* 33: 35-41.
- Norhazrina, N., Wang, J., Hagborg, A., Geffert, J. L., Mutke, J., Gradstein, S. R., Baselga, A., Vanderpoorten, A., and Patiño, J. 2016. Tropical bryophyte floras: A homogeneous assemblage of highly mobile species? Insights from their spatial patterns of beta diversity. *Bot. J. Linn. Soc.* 183: 16-24.
- Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. *J. Linn. Soc. Bot.* 104: 281-291.
- Odu, E. A. 1979. Spore germination in two tropical mosses: *Fissidens* sp. and *Racopilum* sp. *Ann. Bot. (London)* 44: 147-152.
- Odu, E. A. 1981. Reproductive phenology of some tropical African mosses. *Cryptog. Bryol. Lichénol.* 2: 91-99.
- Odu, E. A. 1982. Phenology of west tropical African mosses. *J. Hattori Bot. Lab.* 52: 283-285.
- Odu, E. A. 1987. On the gemmae of west tropical African mosses. *Symp. Biol. Hung.* 35: 215-225.
- Odu, E. A. and Owotomo, O. O. 1982. Periodic production of gemmiferous leaves in two west tropical African *Calymperes* species: *C. afzelii* Sw. and *C. erosum* C. Muell. *Bryologist* 85: 239-242.
- Olarinmoye, S. O. 1974. Ecology of epiphyllous liverworts: Growth in three natural habitats in Western Nigeria. *J. Bryol.* 8: 275-289.
- Olarinmoye, S. O. 1986. Aspects of survival strategies in three common mosses in Ibadan, Nigeria. *Cryptog. Bryol. Lichénol.* 7: 213-218.
- Oliveira, S. M. and Pôrto, K. C. 2001. Reproductive phenology of the moss *Sematophyllum subpinnatum* in a tropical lowland forest of north-eastern Brazil. *J. Bryol.* 23: 17-21.
- Oliveira, S. M. and Pôrto, K. C. 2005. Sporophyte production and population structure of two species of Pottiaceae in an Atlantic Forest remnant in Pernambuco, Brazil. *Cryptog. Bryol.* 26: 239-247.
- O'Shea, B. J. 1989. A guide to collecting bryophytes in the tropics. *British Bryological Society Special Volume No. 3*: 1-30. British Bryological Society, Cardiff.
- Pardow, A. and Lakatos, M. 2013. Desiccation tolerance and global change: Implications for tropical bryophytes in lowland forests. *Biotropica* 45: 27-36.
- Pardow, A., Gehrig-Downie, C., Gradstein, S. R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. *Biodiv. Conserv.* 21: 3637-3655.
- Patiño, J., Bisang, I., Hedenäs, L., Dirkse, G., Bjarnason, Á. H., Ah-Peng, C., and Vanderpoorten, A. 2013. Baker's law and the island syndromes in bryophytes. *J. Ecol.* 101: 1245-1255.
- Patiño, J., Weigelt, P., Guilhaumon, F., Kreft, H., Triantis, K. A., Naranjo-Cigala, A., Sólymos, P., and Vanderpoorten, A. 2014. Differences in species-area relationships among the major lineages of land plants: A macroecological perspective. *Global Ecol. Biogeogr.* 23: 1275-1283.
- Patiño, J., Carine, M., Mardulyn, P., Devos, N., Mateo, R. G., González-Mancebo, J. M., Shaw, A. J., and Vanderpoorten, A. 2015. Approximate Bayesian computation reveals the crucial role of oceanic islands for the assembly of continental biodiversity. *Syst. Biol.* 64: 579-589.
- Piippo, S. 1992. On the seasonal reproduction of *Plagiochila pluma* Steph. *Trop. Bryol.* 5: 7-9.
- Pócs, T. 1976. Correlations between the tropical African and Asian bryofloras, I. *J. Hattori Bot. Lab.* 41: 95-106.

- Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Scient. Hung.* 26: 143-167.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 59-104.
- Pócs, T. 1987. Changes in the biomass and productivity of bryophytes in East African rainforests. XIV Internat. Bot. Congress Abstracts: 264.
- Poore, M. E. D. 1955. The use of phytosociological methods in ecological investigations: I. The Braun-Blanquet System. *J. Ecol.* 43: 226-244.
- Pôrto, K. C. and Oliveira, S. M. 2002. Reproductive phenology of *Octoblepharum albidum* (Bryopsida, Leucobryaceae) in a tropical lowland forest of north-eastern Brazil. *J. Bryol.* 24: 291-294.
- Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In Smith, A. J. E. (ed.). *Bryophyte Ecology*, Chapman and Hall, London, pp. 333-382.
- Proctor, M. C. F. 1990. The physiological basis of bryophyte production. *Bot. J. Linn Soc.* 104: 61-77.
- Proctor, M. C. F. 2002. Ecophysiological measurements on two pendulous forest mosses from Uganda, *Pilotrichella ampullacea* and *Floribundaria floribunda*. *J. Bryol.* 24: 223-232.
- Reenen, G. B. A. van. 1987. Altitudinal bryophyte zonation in the Andes of Colombia: A preliminary report. *Symp. Biol. Hung.* 35: 631-637.
- Reenen, G. B. A. van and Gradstein, S. R. 1983. Studies on Colombian cryptogams. XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Bot. Neerl.* 32: 163-175.
- Richards, P. W. 1952. *The Tropical Rain Forest, An Ecological Study*. University Press, Cambridge, 450 pp.
- Richards, P. W. 1984a. The ecology of tropical forest bryophytes. In: Schuster, R. M. (ed.). *New Manual of Bryology Vol. 2*. Hattori Botanical Laboratory, Miyazaki, Japan, pp. 1233-1270.
- Richards, P. W. 1984b. Introduction. In Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*, Academic Press, New York, pp. 1-8.
- Richards, P. W. 1988. Tropical forest bryophytes. *Synusia* and strategies. *J. Hattori Bot. Lab.* 64: 1-4.
- Rydin, H., Goffinet, B., and Shaw, A. J. 2009. Population and community ecology of bryophytes. In: Shaw, A. J. and Goffinet, B. (eds.). *Bryophyte Biology*. 2nd ed. Cambridge University Press, Cambridge, pp. 393-444.
- Schiffner, V. 1900. *Die Hepaticae der Flora von Buitenzorg*, Erster Band. Brill, Leiden.
- Schuster, R. M. 1969. Problems of antipodal distribution in lower land plants. *Taxon* 18: 46-91.
- Schuster, R. M. 1988. Ecology, reproductive biology and dispersal of the Hepaticae in the Tropics. *J. Hattori Bot. Lab.* 64: 237-269.
- Shaw, A. J., Cox, C., and Goffinet, B. 2005. Global patterns of moss diversity: Taxonomic and molecular inferences. *Taxon* 54: 337-352.
- Sillett, S. C., Gradstein, S. R., and Griffin, D. III. 1995. Bryophyte diversity of *Ficus* tree crowns from cloud forest and pasture in Costa Rica. *Bryologist* 98: 251-260.
- Silva-e-Costa, J. D. C., Luizi-Ponzo, A. P., Resende, C. F. D., and Peixoto, P. H. P. 2017. Spore germination, early development and some notes on the effects of in vitro culture medium on *Frullania ericoides* (Nees) Mont. (Frullaniaceae, Marchantiophyta). *Acta Bot. Brasil.* 31, available at <http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0102-33062017000100019>.
- Song, L., Liu, W. Y., and Nadkarni, N. M. 2012. Response of non-vascular epiphytes to simulated climate change in a montane moist evergreen broad-leaved forest in southwest China. *Biol. Conserv.* 152: 127-135.
- Spruce, R. 1884-1885. *Hepaticae Amazonicae et Andinae*. Transactions et Proceedings of the Botanical Society of Edinburgh 15: 1-588. [published in two parts, the first in 1884 as 15(1): 1-308, the second in 1885 as 15(2): 309-588].
- Spruce, R. (1908) *Notes of a botanist on the Amazon and the Andes*. MacMillan, London, UK.
- Spruce, R. and Wallace, A. R. 1908. *Notes of a botanist on the Amazon and Andes*. Macmillan & Co., London, 2 vols.
- Steere, W. C. 1970. Bryophyte studies on the irradiated and control sites in the rainforest at El Verde, Puerto Rico. In: Odum, H. T. (ed.). *A tropical rainforest: A study of irradiation and ecology at El Verde, Puerto Rico*. Atomic Energy Commission, Washington, D.C.
- Thiers, B. M. 1988. Morphological adaptations of the Jungermanniales (Hepaticae) to the tropical rainforest habitat. *J. Hattori Bot. Lab.* 64: 5-14.
- Thompson, S. L., Yates, D. J., and Bergstrom, D. M. 1994. Water holding capacity of epiphytic bryophytes in subtropical forests. *Austral. Bryol. News.* 31: 6.
- Wagner, S., Bader, M. Y., and Zotz, G. 2014. Physiological ecology of tropical bryophytes. In: Hanson, D. T. and Rice, S. K. (eds.). *Photosynthesis in Bryophytes and Early Land Plants*. Springer, Dordrecht, pp. 269-289.
- Waite, M. and Sack, L. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytol.* 185: 156-172.
- Wang, J., Vanderpoorten, A., Hagborg, A., Goffinet, B., Laenen, B., and Patiño, J. 2016. Evidence for a latitudinal diversity gradient in liverworts and hornworts. *J. Biogeogr.* 44: 487-488.
- Weber, W. A. 1985. Effects on cryptogamic vegetation (lichens, mosses and hepatics). In: *El Niño en la Islas Galápagos: El evento de 1982-1983*. Fundación Charles Darwin para las Islas Galápagos. Quito, Ecuador, pp. 343-361.
- Whittaker, R. J. and Fernández-Palacios, J. M. 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press, Oxford, 402 pp.
- Wikum, D. A. and Shanholtzer, G. F. 1978. Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. *Environ. Mgmt.* 2: 323-329.
- Wilding, N., Hedderson, T., Ah-Peng, C., and Magombo, I. 2016. *Bryophytes of Kenya's Coastal Forests. A Guide to the Common Species*. Published by authors in electronic format, 66 pp.
- Zander, R. H. and During, H. J. 1999. *Neophoenix* (Pottiaceae), a new African moss species found through soil diaspore bank analysis. *Taxon* 48: 657-662.
- Zanten, B. O. van. 1978. Experimental studies on trans-oceanic long-range dispersal of moss spores in the Southern Hemisphere. *J. Hattori Bot. Lab.* 44: 455-482.

- Zanten, B. O. van and Gradstein, S. R. 1987. Feasibility and long-distance transport in Colombian hepatics, preliminary report. *Symp. Biol. Hung* 35: 315-322.
- Zanten, B. O. van and Gradstein, S. R. 1988. Experimental dispersal geography of Neotropical liverworts. *Beih. Nova. Hedw.* 89: 41-94.
- Zanten, B. O. van and Pócs, T. 1981. Distribution and dispersal of bryophytes. *Adv. Bryol.* 1: 479-562.
- Zartman, C. E. 2004. Habitat fragmentation and epiphyllous bryophytes in a central Amazonian forest. Ph.D. thesis, Duke University, Durham, NC.
- Zotz, G. and Bader, M. Y. 2008. Epiphytic plants in a changing world – Global change effects on vascular and non-vascular epiphytes. *Progress in Botany* 70: 147-170.
- Zotz, G., Büdel, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO₂ exchange of tropical bryophytes in a lower montane rain forest in Panama. *Bot. Acta* 110: 9-17.

CHAPTER 8-2

TROPICS: GEOGRAPHIC DIVERSITY DIFFERENCES

TABLE OF CONTENTS

Diversity - Geographic Differences	8-2-2
Africa	8-2-6
Asia and Australia	8-2-9
Neotropics	8-2-16
Endemism	8-2-28
Africa	8-2-30
Asia	8-2-31
Neotropics	8-2-32
Causes of Endemism	8-2-34
Dangers to Endemics	8-2-34
Tropical Rainforests	8-2-35
Pantropical Distributions	8-2-36
Substrate Specificity	8-2-37
Forest Floor	8-2-38
Rock Houses	8-2-39
Summary	8-2-39
Acknowledgments	8-2-39
Literature Cited	8-2-40

CHAPTER 8-2

TROPICS: GEOGRAPHIC DIVERSITY DIFFERENCES



Figure 1. Rainforest in Borneo. Photo by Duke Abruzzi, through Creative Commons.

Diversity – Geographic Differences

Only in the 21st century are we seeing publications with keys that cover broad areas or a wide range of taxa in the tropics, especially the Neotropics. This lack of taxonomic understanding has hindered our understanding of diversity and geographic differences.

Among these recent publications, the publication by Gradstein *et al.* (2001) dealing with all bryophytes of the Neotropics (mosses, liverworts, hornworts) is notable. In addition, there is a large series of floras dealing with Neotropical mosses (for a list see Gradstein *et al.* 2001), fewer on liverworts (Gradstein & Costa 2003; Gradstein & Ilkiu-Borges 2009). For Africa, a broad spectrum moss key has been translated from 1978, lacking modern familial

classifications, but is somewhat comprehensive (Petit 1992). More recent treatments on liverworts and hornworts was published for West Africa by Jones *et al.* (2004), based on an unpublished flora manuscript of the specialist of African liverworts E. W. Jones, and for Rwanda by Fischer (2013), including keys to genera and species and many color photos. For the southwestern part of Asia (Arabia) one can use the treatise by Kürschner and Frey (2011), for Singapore mosses by Tan *et al.* (2008) and for liverworts and hornworts of Java by Gradstein (2011). Other treatments are available for China and Japan, where bryology has long been studied, but publications were mostly in the native languages until recently. Recent publications include dozens of good floristic papers by young bryologists from the tropical countries, for example

from Brazil, Bolivia, Venezuela, Costa Rica, Puerto Rico, Guadeloupe, but also West Africa, Reunion, Madagascar and Malaysia.

Hedenäs (2007) used checklists from 78 countries to determine the global diversity patterns of pleurocarpous mosses. He found that most of this moss diversity occurred outside the Holarctic area. Rather, the tropics have an especially diverse pleurocarpous moss flora. Furthermore, species turnover among pleurocarpous mosses is higher in the tropics than in the temperate zone.

It is not surprising that the greatest number of bryophyte species occurs in the tropics, with one-third of the Earth's flora occurring in the tropical Americas alone (Gradstein 1995a, b; Gradstein *et al.* 2001). Nevertheless, there are fewer species of mosses in the tropics than in the temperate zone; it is the liverworts and hornworts that reach their peak of species here. Delgadillo (1998) reported 3,900 species of mosses recorded from the Neotropics but considered that the real number, taking into account taxonomic revisions, might be considerably lower. Gradstein *et al.* (2001) accepted about 2,600 species of mosses, 1,350 of liverworts, and 30 of hornworts in the region, and this number may further fluctuate due to synonymy and new discoveries. This number is commensurate with the high diversity of flowering plants (90,000) in the Neotropics, compared to 250,000 species of flowering plants worldwide (Churchill *et al.* 1995a). Frahm (1995) compared the European, tropical African, and Neotropical moss floras, a task that provides the knowledge base for many kinds of ecological studies.

On the other hand, estimates of the number of bryophyte species in the tropics is compromised by the large number of synonyms in the literature. For example, *Frullania atrata* (Figure 2) has been widely misinterpreted in the literature and has been confused with other *Frullania* species, whereas the true *F. atrata* is rare (Uribe & Gradstein 2003; Gradstein, pers. comm. 9 September 2018). The common Neotropical *Marchantia chenopoda* (Figure 3-Figure 4) has 15 synonyms (Bischler 1984) and the common pantropical moss *Leucomium strumosum* (Figure 5) has almost 30 synonyms from all over the tropics (Allen 1987). Such synonymy is mostly the result of researchers in different parts of the world naming a species as new because of inadequate knowledge of or access to bryophytes in other locations.

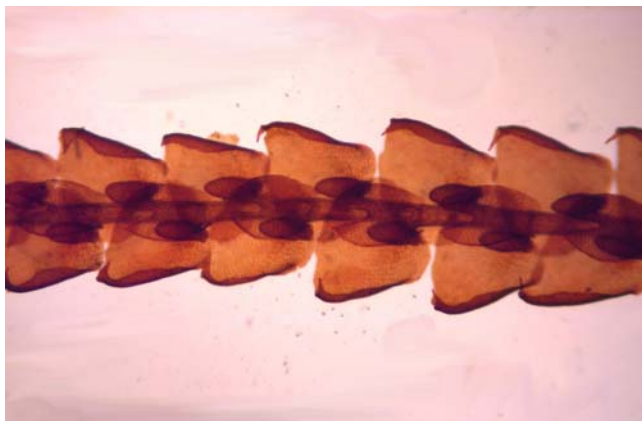


Figure 2. *Frullania atrata*, a species name that has been used for many similar *Frullania* species. Photo by Juan Larrain, with permission.



Figure 3. *Marchantia chenopoda* with antheridiophores, a Neotropical species in a genus with many tropical synonyms. Photo by Janice Glime.



Figure 4. *Marchantia chenopoda* females. Photo by Martin Nebel, courtesy of Robbert Gradstein.



Figure 5. *Leucomium strumosum*, a tropical species with almost 30 synonyms. Photo by Claudio Delgadillo Moya, with permission.

Tropical liverworts in the families *Lejeuneaceae* (Figure 6), *Frullaniaceae* (Figure 7-Figure 8), *Radulaceae* (Figure 9-Figure 10), *Plagiochilaceae* (Figure 11), and *Lepidoziaceae* (Figure 12) predominate among the liverworts, with lesser numbers in *Metzgeriaceae* (Figure 13) and *Aneuraceae* (Figure 14) (Schuster 1988). Gradstein (1995a) suggests that the liverwort genus *Plagiochila* (Figure 11), with hundreds of species in tropical montane forests, is generally considered the most

diverse liverwort genus. Pendent taxa are common on branches and tree trunks of the montane forests.



Figure 6. *Cololejeunea truncatifolia* (Lejeuneaceae) from Uganda. Photo by Martin Wigginton, with permission.



Figure 7. *Frullania* (Frullaniaceae) in the Neotropics. Photo by Michael Lüth, with permission.



Figure 8. *Frullania* (Frullaniaceae) in the Neotropics. Photo by Michael Lüth, with permission.



Figure 9. *Radula buccinifera* on a tree in the Asian tropics. Photo by David Tng <www.davidtng.com>, with permission.



Figure 10. *Radula cf. voluta* (Radulaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 11. *Plagiochila adianthoides* (Plagiochilaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 12. *Lepidozia* sp. (Lepidoziaceae), a common tropical family of leafy liverworts. Photo by Ken-ichi Uedo, through Creative Commons.



Figure 13. *Metzgeria uncigera* (Metzgeriaceae), a common tropical family of liverworts. Photo by Blanka Aguero, with permission.



Figure 14. *Riccardia multifida* (Aneuraceae), representing a common tropical family. Photo by Hermann Schachner, through Creative Commons.

Despite all these cautions about conspecific taxa that have been given multiple names in multiple locations, DNA genetics may once again expand the species number. For example, Dong *et al.* (2012) analyzed molecular data from the epiphyllous liverwort *Diplasiolejeunea* (Figure 15-Figure 16). This is a pantropical genus that occurs from lowlands to more than 4,000 m altitude. This indicated that the evolutionary diversity of the genus based on morphology alone has been underestimated. The molecular data indicate a distinct split between the Neotropical and

Palaeotropical (Old World) clade, with two predominantly Neotropical subgenera [*Austrolejeuneopsis* and *Diplasiolejeunea* (Figure 15) with the former containing mainly epiphytic species, the latter mainly epiphylls] and one predominantly Palaeotropical subgenus, *Physolejeunea* (Figure 16), an epiphytic montane subgenus.



Figure 15. *Diplasiolejeunea brunnea* (subgenus *Diplasiolejeunea*) in Ecuador on leaf. Photo courtesy of Tamás Pócs.



Figure 16. *Diplasiolejeunea plicatilobula*, in the epiphytic montane subgenus *Physolejeunea*. Photo by David Tng, with permission.

Checklists of the tropics are listed in Frahm *et al.* (2003). For the geographic areas treated in this chapter, the number of references given are probably less than representative, but are listed to help researchers get started on the areas. More recent references have been included only as I have discovered them, with much help from Robert Gradstein.

Frahm *et al.* (2003) estimated that about 8,000 species of bryophytes occur in the tropics, comprising half to two-thirds of all the bryophyte species in the world. The European flora has only about 1,600 species that one can find in 32 floras. For the tropics, as of 2003, only 16 floras existed. As will be seen in the following subchapters, the liverworts and hornworts are much more abundant and occupy a much higher percentage of the bryophyte flora in the tropics compared to other regions of the world. Nevertheless, many areas remain unexplored or poorly explored, so numbers of species and numbers of **endemics**

(known only from a limited area) should be compared with caution.

Norhazrina *et al.* (2016) considered the **beta diversity** [ratio between gamma (regional) and alpha (local) diversities] of bryophytes in the tropics. They examined the beta diversity of 7485 tropical moss species and 3276 tropical liverwort and hornwort species in 164 and 154 operational geographical units, respectively. They found a "slight but significantly higher beta diversity among than within tropical regions." They concluded that oceans provide a significant barrier to the routine dispersal, even for the easily dispersed bryophytes, causing large-scale floristic patterns.

The following sections on diversity and endemism are mostly historic. Hence, numbers are likely to be out-dated. They are designed to provide the background and explain why ecological studies in the tropics are occurring only recently.

Africa

Africa is a continent with a wide range of tropical habitats, from dry desert of the Sahara to the 5,895 m summit of Mt. Kilimanjaro. The climate ranges from tropical to subarctic, but much of the land is desert, particularly the northern half.

One of the earliest recorded observations relating to ecology of the African desert is that of Mungo Park. As quoted in Crum (1983), Park was crossing 3220 km of unknown land and African desert when he reported "I considered my fate as certain, and that I had no alternative but to lie down and perish... At this moment, painful as my reflections were, the extraordinary beauty of a small moss in fructification irresistibly caught my eye." Stark (1860) captured the story in this poem (author not specified):

*Sad, faint, and weary on the sand
Our traveller sat him down; his hand
Cover'd his burning head.
Above, beneath, behind, around,
No resting for the eye he found;
All nature see'd as dead.*

*One tiny tuft of moss alone
Mantling with freshest green a stone
Fix'd his delighted gaze;
Through bursting tears of joy he smiled
And while he raised the tendril wild
His lips o'erflowed with praise*

*O! shall not He who keeps thee green,
Here in the waste, unknown, unseen,
Thy fellow-exile save?
He who commands the dew to feed
Thy gentle flower, can surely lead
Me from a scorching grave.*

Mungo Park lived to tell the tale and a specimen of this lowly moss was later identified as a species of *Fissidens* in

the *F. bryoides* (Figure 17) group. This genus is particularly common in Africa, with ~90 known species out of 450 worldwide (Bruggeman-Nannenga, 2013a, b), with a new one soon to be published from termite mounds (Bruggeman-Nannenga in press; Ezukanma *et al.* in prep.).



Figure 17. *Fissidens bryoides*, possibly the moss found by Mungo Park, or one of its close relatives. Photo by Hermann Schachner, through Creative Commons.

O'Shea (1995) provided an early checklist of the mosses of sub-Saharan Africa (Figure 18), listing 2939 species, based on the literature, and indicating distribution by country. While he updated some of the nomenclature, naming new combinations, much remained to straighten out the duplication in names around the continent.



Figure 18. Sub-Sahara Africa. Photo from CIFOR, through Creative Commons.

Ros *et al.* (1999) provided a checklist of northern Africa. It is striking that only 171 liverwort species were known, compared to 706 of mosses. It is likewise remarkable that only 4 taxa were known from the Republic of Mali or Niger. Wigginton (2001b) noted that *Eucladium verticillatum* is widespread in Mali, where it is encrusted with **tufa** (variety of limestone formed when carbonate minerals precipitate out of ambient temperature water).

Pócs, with his coworkers, has been a lifelong contributor to the bryophyte flora of Africa. Among his earlier contributions was a joint paper (Bizot & Pócs 1974) on bryophytes of East Africa, based on collections from a number of bryologists, himself included. This included 441 species, of which 115 were new for East Africa and 4

for all of tropical Africa and 30 were new for all of continental Africa. Other studies reporting on African bryophytes include Arnell (1956 – East African Mountains – liverworts), Bizot & Pócs (1974, 1979, 1982 – East Africa), Pócs (1990, 2011 – East Africa), Kürschner & Onraedt (1990 – Republic of Djibouti), Grolle [1993 – Zaire and Rwanda – **Pallaviciniaceae** (Figure 19), **Haplomitriaceae** (Figure 20)], and Miehe & Miehe (1994 – Ethiopia).



Figure 19. *Symphogyna brasiliensis* female from the Neotropics. This family **Pallaviciniaceae** also occurs in Africa. Photo by George Shepherd, through Creative Commons.



Figure 20. *Haplomitrium hookeri*; **Haplomitriaceae** are among the liverworts known from Zaire and Rwanda. Photo by Des Callaghan, with permission.

In an update of his earlier checklist, O'Shea (1997a, b) reported 3,048 taxa from sub-Saharan Africa (Figure 18), but suggested that it will probably be reduced to ~1300 species by revisions. Based on an expedition of the British Bryological Society to the Mulanje Mountain (Figure 21), Wigginton (2001a) reported 64 taxa in the single leafy liverwort family of **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). This report acknowledged 47 species new to Malawi, emphasizing how poorly we knew the bryophyte flora in so many tropical areas. Frahm (2003) bemoaned the lack of studies in Africa and the likely number of synonyms. Such taxonomic and floristic studies and

compilations as these laid the foundation that permitted ecological work to begin.



Figure 21. Mount Mulanje, Africa. Photo by David Davies, through Creative Commons.

Not all of the African tropics have a high bryophyte diversity. In three locations in the Ekiti State, Nigeria (Figure 22), 69 samples yielded only 8 species of mosses (Adebiyi & Oyeyemi (2013), two of which were among those studied by Odu (1981, 1982) in Nigeria for their reproductive phenology: **Pelekium gratum** (syn.=*Thuidium gratum*; Figure 23) and **Racopilum africanum** (Figure 24). A study of bryophytes in the Eastern Nigerian Highlands yielded only 27 bryophyte taxa – 22 mosses, 5 liverworts (Ezukanma *et al.* 2017).

Oyesiku (2012) reviewed the Nigerian bryophytes, including a discussion of uses. His was one of the few attempts to assess the importance of bryophytes to agriculture and the effects that agriculture is having on the bryophytes. He expressed concern that so few people are working on Nigerian bryophytes.



Figure 22. Ikole Town, Ekiti State. Photo by Tijae07, through Creative Commons.



Figure 23. *Pelekium gratum*, a tropical Nigerian moss. Photo by Shyamal L., through Creative Commons.



Figure 25. *Cupressus macrocarpa*. Photo by Ames, through Creative Commons.



Figure 24. *Racopilum africanum* with capsules, a tropical Nigerian moss. Photo by Jan-Peter Frahm, with permission.

Few studies seem to be available from Ghana. Hodgetts *et al.* (2016) reported on the bryophytes of the Atewa Forest in eastern Ghana. The region is highly threatened by farming, hunting, and illegal mining. Hodgetts and coworkers explored the swamp forest and upland evergreen forest where they expected the greatest bryophyte richness. They identified 164 species, 58 of which were new to Ghana.

The cover of bryophytes differs markedly, dependent on light availability, litter cover, and climate. Petit and Symons (1974) found that in the planted woods of *Cupressus* (Figure 25) and *Acacia* (Figure 26) in Burundi (an east African country with an equatorial climate), the ground surface is mostly covered with bryophytes. Nevertheless, in 17 woods, only 28 species were found, and only 15 of these were typical for that habitat.



Figure 26. *Acacia*; forest floors of *Acacia* are covered by bryophytes in Burundi. Photo from pxhere, through Creative Commons.

To demonstrate just how poorly some African floras are known (Hylander *et al.* 2010), we need only look at the new records from the biosphere reserve of Kafa in Ethiopia (Figure 27). A team of 29 experts, but no bryologists, spent 10 days collecting plants (Müller & Flügel 2016). They did, however, bring some bryophyte specimens back. While this yielded only 13 liverwort and 24 moss species, it revealed 5 mosses not previously known from Ethiopia!

Hylander *et al.* (2010) found 89 species of liverworts, of which 41 were new to Ethiopia (Figure 27), further emphasizing that bryological explorations have been inadequate there. Among these are many epiphyllous species that are typically sensitive to drought. These are mostly along streams where humidity remains higher. The family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) is the most common family, with several representatives in other families, including **Frullaniaceae** (Figure 2, Figure 7-Figure 8), **Plagiochilaceae** (Figure 11), and **Radulaceae** (Figure 9-Figure 10).

In a more recent study, Hylander *et al.* (2017) found 139 moss species in montane forests of Ethiopia (Figure 28), of which 53 are newly reported for the country. *Meteoriopsis reclinata* (Figure 29) is a new record for Africa.



Figure 27. Forest with native carrying firewood in Kafa, Ethiopia. Photo by Rod Waddington, through Creative Commons.



Figure 28. Semien Mountains, Ethiopia. Photo by Hulivili, through Creative Commons.

Hedderson *et al.* (2015) added to the list of bryophytes from Mabu Mountain in Mozambique, based on collections from non-bryologists. They were able to identify 56 species, of which 43 were new records for the country. The authors considered this small sampling of the country to be indicative of its bryophyte diversity and the need for more study.

Marline *et al.* (2012) provided an updated checklist of Madagascar bryophytes. This updated list revealed 751 moss, 390 liverwort, and 3 hornwort taxa. Of these, ~29% are endemic.

Reunion Island provides an interesting ecological site. It has diverse habitats of lava flows and large topographic relief. Ah-Peng *et al.* (2010) brought the total number of

species and infraspecific taxa to 776 in 2010 with the addition of 123 taxa. They considered the presence of a high altitudinal gradient and high rainfall regime, coupled with relatively short distance to East Africa, to account for the large number of species on an island with only 2512 km².



Figure 29. *Meteoriopsis reclinata* was a new record for Africa in 2017. Photo by Niels Klazenga, with permission.

Several studies have compared the bryophyte floras of parts of Africa with other parts of the tropics (Frahm 1995), including Asia (Pócs 1976), and Madagascar (Pócs 1975). Oyesiku (2012) noted the "moribund" state of bryology in Africa.

Asia and Australia

The earliest studies on tropical Asian bryophytes are those in Java. Dozy and Molkenboer produced *Bryologia Javanica* (1856 – vol. 1, 1867 – vol. 2) on the Java mosses. Later Max Fleischer produced a three volume set, the *Moss Flora of Java* (1900-1922). For liverworts, Reinwardt *et al.* (1824) and Nees von Esenbeck (1830) provided the first species lists. These were followed later by the floras of vander Sande Lacoste (1857, 1864) and Schiffner (1900) (in Gradstein 2011). The latter work remained unfinished. Most recently, Gradstein (2011) has presented the Guide to the Liverworts and Hornworts of Java, covering nearly 200 years of bryological studies in Java. Approximately 1000 species of bryophytes are now known from Java (Robbert Gradstein, pers. comm. 9 September 2018). The presence of a biological research station at Cibodas (Figure 30) in Indonesia, founded by the Dutch around 1890 in the montane rainforest belt, has been of enormous help in accomplishing these bryological studies, including also work by Schiffner, Goebel, Giesenhausen, Verdoorn, and others.



Figure 30. Botanical garden in Cibodas, Indonesia. Photo by Hullie, through Creative Commons.

One of the early Asian studies was that of Dixon (1935) who reported on the moss flora of Borneo. Other studies on Asian tropics in China and Japan have been unavailable to people from other countries because they were published in the native languages and not understood by others. In some cases political boundaries and cultural differences complicated the ability of bryophyte ecologists to conduct studies. Redfearn (1990) points out that many of the early studies in China have been lost during the Cultural Revolution. And isolationism led to much synonymy, even within China. At that time he noted that much study was needed. Now there are many bryologists in China, but work is still needed on the many diverse habitats that define the country.

Asia has the most generic and familial diversity in the tropics, with many taxa that occur only in the Asian tropics. Africa, on the other hand, has few taxa of its own and little liverwort diversity, as we currently understand the flora. In the Americas, there are fewer unique moss taxa, but the liverworts are more diverse, with cover of liverworts in montane forests exceeding that of the mosses.

Unique to Asia are the large **Dawsoniaceae** (Figure 31), **Garovagliaceae** (Figure 32), **Hypnodendraceae** (Figure 33), and **Spiridentaceae** (Figure 34) among mosses (Gradstein & Pócs 1989). Asia is the center for distribution of a number of tropical taxa in a variety of families and is home to the **epiphyllous** (living on leaves) moss **Ephemeropsis** (Figure 35) and liverwort **Metzgeriopsis** (Figure 36). Again, members of the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) dominate the liverworts, but with a number of different genera. The African flora is less rich and has few elements of its own. Typical mosses in the Asian rainforest (Figure 37) are **Leucoloma** (**Dicranaceae**;

Figure 38), **Cryphaeaceae** (Figure 39), **Rutenbergiaceae**, **Hildebrandtiella** (Figure 40) and **Renauldia** (**Pterobryaceae** – see Figure 134), and in both lowlands and montane regions, **Fissidens** (Figure 41). Among the liverworts, **Lepidozia** (Figure 12; subgen **Sprucella**) is most common (vanden Berghen 1983; Gradstein & Pócs 1989).



Figure 31. *Dawsonia superba*, a species in the common Asian tropical family **Dawsoniaceae**. Photo by Phil Bendle, permission through John Grehan.



Figure 32. *Garovaglia elegans*, a species in the common Asian tropical family **Garovagliaceae**. Photo by Zen Iwatsuki, with permission.



Figure 33. *Hypnodendron vitiense* with capsules, a species in the common Asian tropical family **Hypnodendraceae**. Photo by Marshall Simon, through Creative Commons.



Figure 34. *Spiridens reinwardtii*, a species in the common Asian tropical family **Spiridentaceae**. Photo by Daniel Nikrent, with online permission.



Figure 35. *Ephemeropsis trentepohlioides* with capsules, an Asian tropical species. Photo by David Tng, with permission.



Figure 36. *Metzgeriopsis* growing on a palm leaf on Bukit Larut, Malaysia, 1100-1200 m, with Malaysian bryologist Kien Tai Yong (right). Photo courtesy of Robbert Gradstein.



Figure 37. Misty forest at Emei Shan, China. Photo by McKay Savage, through Creative Commons.



Figure 38. *Leucoloma* sp., a typical rainforest species. Photo by Shyamal L., through Creative Commons.



Figure 39. *Cryphaea heteromalla*, a typical rainforest species. Photo by Tim Waters, through Creative Commons.



Figure 40. *Hildebrandtiella guyanense* from the Neotropics, in a typical rainforest genus. Photo by Michael Lüth, with permission.



Figure 41. *Fissidens asplenioides*, in a genus that is found in both lowlands and montane regions. Photo by L. Jensen, University of Auckland, with online permission.

Gradstein (1991) summarized the known Asian **Ptychanthoideae** (Figure 42) in the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). This group was represented by 88 species in 17 genera, having fewer genera but more species than this group in the Neotropics. Gradstein suggested that the greater number of species in Asia might be the result of the greater latitudinal extension of the rainforest in the Far East. That region has 22% non-tropical species of **Ptychanthoideae** compared to less than 2% in the Neotropics. It could also represent greater early exploration.



Figure 42. The tropical leafy liverwort *Ptychanthus striatus*. Photo by Li Zhang, with permission.

In Malaysia (Figure 43-Figure 44), the diverse vegetation consists of swampy mangroves, extensive river floodplains, dipterocarp forests, and montane forests (Chuah-Petiot 2011). **Altimontane** (montane grasslands, shrublands, and woodlands; Figure 44) communities occur on Mt. Kinabalu in Sabah above 3300 m asl, with average temperatures from 6° to 10°C. The tropical climate of Malaysia ranges in temperature from 21° to 32°C; annual rainfall is from 2000 mm to 3500 mm.

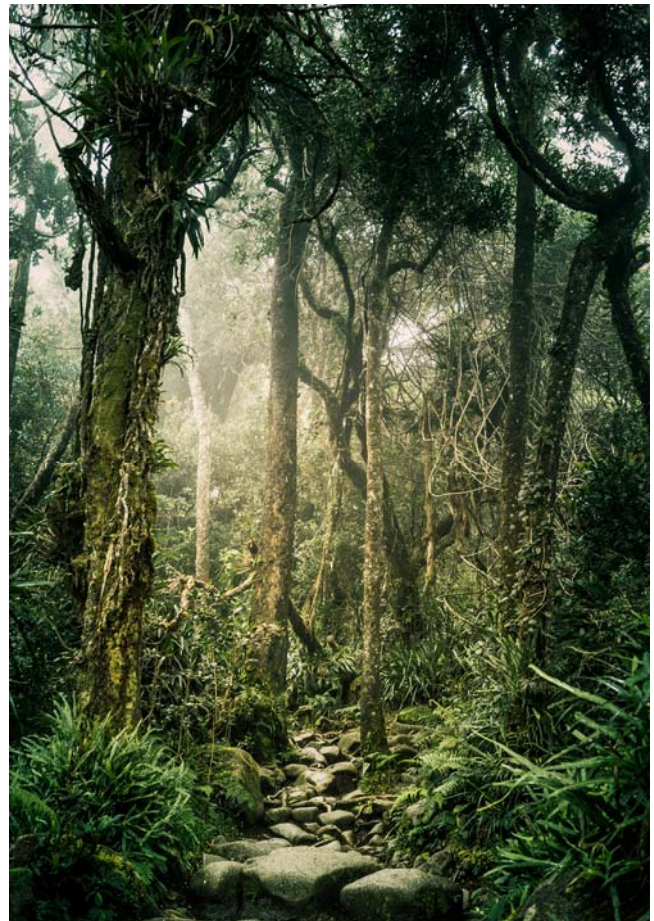


Figure 43. Malaysian Pathway to Mount Kinabalu. Photo by Arto Marttinen <Wandervisions.com>, through Creative Commons.



Figure 44. Mt. Kinabalu altimontane zone. Photo through Creative Commons.

Malaysian (Figure 45) liverwort studies can be traced to the year 1838 (Lee *et al.* 2018). Most of the collections have been made from 1950 to 2000, with many new taxa described. In a recent paper, Chuah-Petiot (2011) published a checklist of liverwort and hornwort species and infra-specific taxa, citing 758 liverworts and 6 hornworts. The **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) far outnumber the other liverwort families (282 taxa), as found also in the study by Pócs and Chantanaorrapint (2016) in Thailand, where 30 out of 38 liverworts were in the **Lejeuneaceae**. In Malaysia, Chuah-Petiot found that species richness of the **Lejeuneaceae** was followed by **Lepidoziaceae** (110, Figure 12), **Frullaniaceae** (67; Figure 2, Figure 7-Figure 8), **Plagiochilaceae** (52; Figure 11), **Geocalycaceae** (36; Figure 46), **Lophoziaceae** (35; Figure 47), and **Radulaceae** (35; Figure 9-Figure 10). As in many areas of the tropics, the genera with the most Malaysian species are *Cololejeunea* (84; Figure 48), *Frullania* (67; Figure 2, Figure 7-Figure 8), *Bazzania* (53; Figure 49, Figure 104), *Plagiochila* (47; Figure 11), and *Radula* (35, Figure 9-Figure 10). More recently, Lee *et al.* (2018) reported 747 liverwort species from Malaysia, occupying nearly 15% of the liverwort diversity in the world.

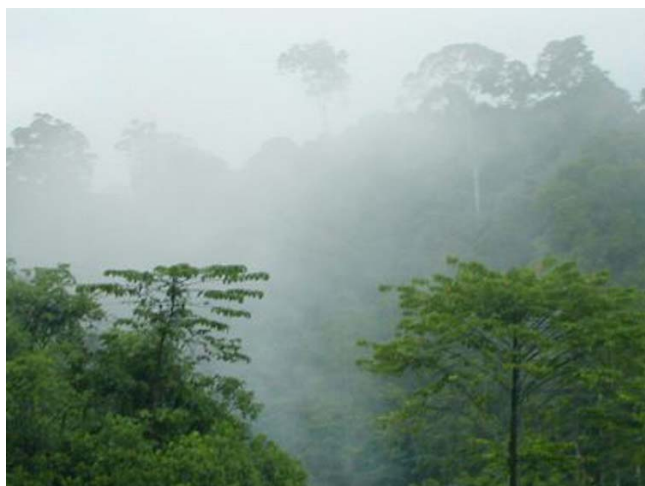


Figure 45. Dermakot Forest Reserve in Malaysia. Photo by Angela Sevin, through Creative Commons.



Figure 46. *Heteroscyphus coalitus*, a member of the **Geocalycaceae**; this family is one of those present in the Atlantic Forest. Photo by Yang Jia-dong, through Creative Commons.



Figure 47. *Lophozia incisa* (**Lophoziaceae**) with perianth. Photo by J. C. Schou, with permission.



Figure 48. *Cololejeunea calcarea*, among the genera with the most species in Malaysia. Photo by Hermann Schachner, through Creative Commons.



Figure 49. *Bazzania* in the Neotropics, among the genera with the most species in Malaysia. Photo by Michael Lüth, with permission.

Among the older studies including mosses of Malaysia (Figure 45) are those of Tixier (1980), Mohamed and Tan (1988), Frahm *et al.* (1990), Inoue (1989), and Akiyama *et al.* (2001). Mohamed and Tan (1988) reported 475 taxa of mosses, a number that has changed with further studies and nomenclatural synonymies. More recently, Suleiman *et al.* (2006) enumerated 582 moss taxa from Sabah, Borneo. Tan and Iwatsuki (1999) considered Mt. Kinabalu (Figure 44, Figure 50) to be one of four diversity hotspots for mosses in Malesia, an area that includes the Malay Peninsula, the Malay Archipelago, New Guinea, and the Bismarck Archipelago. Higuchi *et al.* (2008) found 97 species of mosses, exclusive of pleurocarpous species, on Mt. Kinabalu. Among the rare species there is the moss *Takakia lepidozoides* (Figure 51) near Paka Cave. Higuchi and Lin (2005) found that the size and life form of *Takakia lepidozoides* in Taiwan differ between sheltered and exposed sites. Higuchi and coworkers (2008) found that plants in their open sites on Mt. Kinabalu were larger, forming loose mats, compared to those from sheltered places.



Figure 50. Mount Kinabalu, Borneo. Photo by Nep Grower, through Creative Commons.



Figure 51. *Takakia lepidozoides*, a rare species of moss that occurs on Mt. Kinabalu. Photo through Creative Commons.

Kürschner (2003a) is among the more recent of the Asian researchers. He studied epiphytes in the Asir Mountains of Saudi Arabia and Yemen (see Tropics subchapters on epiphytes). In a second study (Kürschner 2003b), he examined the xeric bryophyte community in Yemen. He described a new association of *Riccia jövet-astiae* with *R. argenteolimbata* and *Barbula unguiculata* (Figure 52). This association occurs typically on the shallow soils overlying volcanic rock outcrops in the *Sterculia africana* (Figure 53) woodland. This area is beset with monsoons. It supports a number of **Ricciaceae** (Figure 54–Figure 55) and **Marchantiaceae** (Figure 3–Figure 4) that are typical or xerotropical Africa. *Riccia atromarginata* var. *jövet-astiae* (see Figure 54) and *R. albolimbata* (Figure 55) are characteristic of this habitat. The life strategies are characterized by shuttle species with large spores, providing for a good diaspore bank.



Figure 52. *Barbula unguiculata*, a species of the xeric community in Yemen. Photo by Bob Klips, with permission.

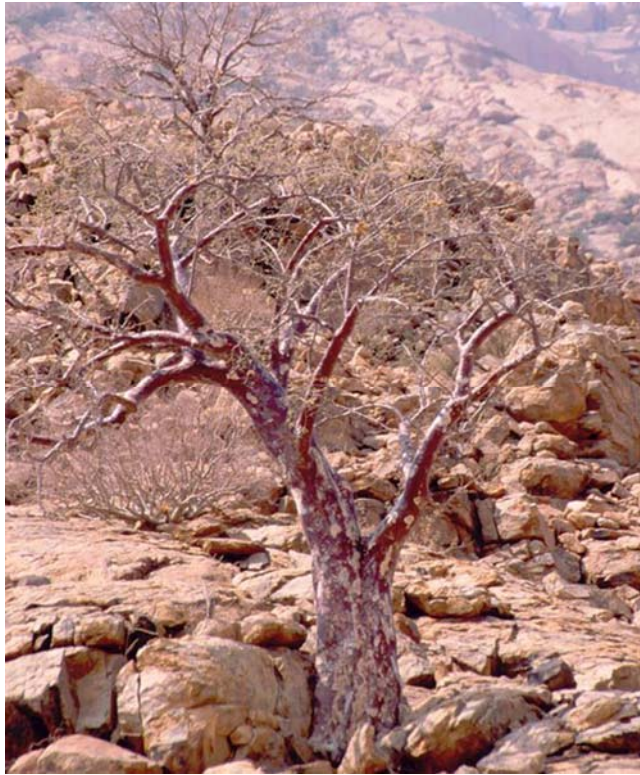


Figure 53. *Sterculia africana* woodland, where shallow soils support xeric bryophytes such as **Ricciaceae** and **Marchantiaceae**. Photo by Joachim Beyenbach, through Creative Commons.



Figure 54. *Riccia atromarginata*, a species found on the thin soils of the *Sterculia africana* woodland. Photo by Jan-Peter Frahm, with permission.

Sukkharak and Chantanaorrapint (2014) summarized the bryophyte studies that have occurred in Thailand (Figure 56). They indicated two periods in bryological studies. In the first period (1899-1977), foreign bryologists were the contributors. In the second period (1977 to present), bryologists from Thailand conducted the studies. These studies resulted in 2 new species of hornworts, 20 of liverworts, and 63 of mosses. Based on studies elsewhere, 48 remain unique to Thailand and may therefore be considered endemic.

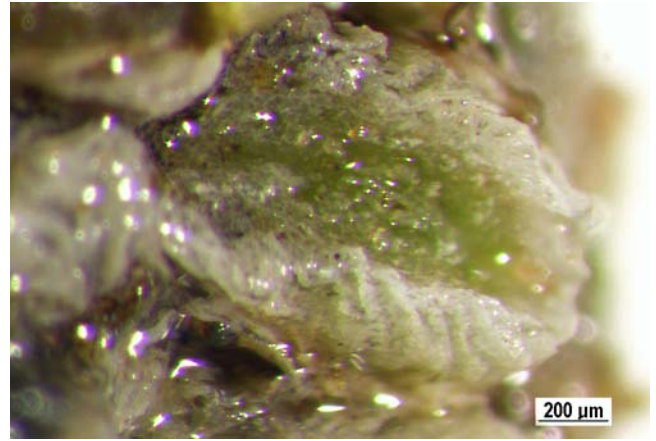


Figure 55. *Riccia albolimbata*, a species found on the thin soils of the *Sterculia africana* woodland. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

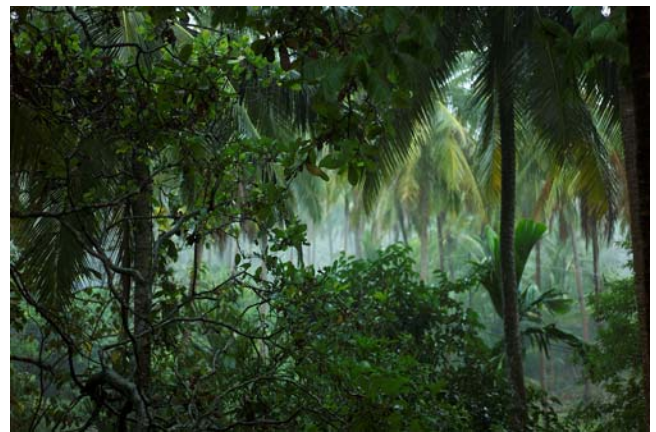


Figure 56. Thai rainforest. Photo by Michael Cory, through Creative Commons.

Many areas of the Asian tropics remain poorly explored for bryophytes. Sulawesi, Indonesia (Figure 57), is among such locations. Steep mountains with dense vegetation make exploration difficult (Rowe *et al.* 2016). In their exploration of the island, Gradstein *et al.* (2005) found 476 species of bryophytes. Four moss species and one liverwort species appear to be **endemic** to the island. But several large genera are unknown from Sulawesi, suggesting that sufficient exploration may be lacking.



Figure 57. South Sulawesi, Indonesia, Mountains. Photo by Achmad Rabin Taim, through Creative Commons.

Few studies seem to be available on Viet Nam (Figure 58) bryophytes. Pócs (1969) surveyed the leafy liverwort genus *Bazzania* (Figure 49, Figure 104). A more comprehensive study by Ninh (1993) recorded 178 taxa. Much more comprehensive work is needed in that country, and ecological work seems to be absent.



Figure 58. Vietnamese valley. Photo by Ottre, through Creative Commons.

Sri Lanka (Figure 59) is likewise an understudied country bryologically. Rubasinghe and Long (2014) reviewed the history of bryological work in the country and remarked on the goal to produce a comprehensive bryophyte flora for Sri Lanka, the first of its kind for the country.



Figure 59. Rainforest in Sri Lanka. Photo by Dan Lundberg, through Creative Commons.

Australia has received much more attention (at least in English publications) than many of the Asian countries. This has permitted ecological and physiological studies to take place. Ramsay and Cairns (2004) contributed a checklist for the Wet Tropics bioregion in northeastern Queensland (Figure 60), listing 398 species. This permitted them to determine the families represented by the most species (Table 1). They elaborated on habitat, distribution, and bryogeographical affinities for the wet

tropics. Ramsay is best known for her genetic work with bryophytes. Cairns has published several papers on interactions with animals. These areas of study have been possible due to the strong taxonomic background that is available (see, for example, Scott 1985). Nevertheless, most of the studies have been in southern Australia where bryophyte-friendly habitats are more common and accessible.



Figure 60. Tropical rainforest in northeastern Australia. Photo by Thomas Schoch, through Creative Commons.

Table 1. Families of mosses exhibiting the highest species richness in the wet tropics of Australia.

Family	Number of genera	Number of species
Bryaceae	5	23
Calymperaceae	7	47
Dicranaceae	7	29
Meteoriaceae	8	13
Sematophyllaceae	16	32

This history is representative of the background necessary to carry out ecological studies on species dominance, community structure, comparative diversity, biomass comparisons, and many other aspects of ecology. It demonstrates the long process needed before ecologists can begin many kinds of studies and helps to explain the paucity of ecological studies in many parts of the tropics.

Neotropics

The **Neotropics** (Figure 61) is synonymous with New World Tropics. It Includes areas of Mexico, Central America, the West Indies, Chocó, Northern Andes, Central Andes, Amazonia, Guyana Highland, Planalto, and Southeastern Brazil (Gradstein *et al.* 2001).

Until relatively recently, any comprehensive guide to the bryophytes of the Neotropics was lacking. Researchers had to find the scattered treatments among individual papers, making comprehensive ecological studies, especially community studies, difficult to impossible. The publication by Gradstein *et al.* (2001) made it possible to expand the types of ecological studies that are feasible.



Figure 61. Neotropics map. The dashed lines mark the borders of the tropics, with Tropic of Cancer in the north and Tropic of Capricorn in the south; the solid straight line is the Equator. Photo from Ökologix, through Creative Commons.

Most studies have been exclusive to either mosses or liverworts. Various studies contributing to these records include, for mosses, Steere 1948 – Ecuador, Pursell 1973 – Venezuela, Bowers 1974 – Costa Rica, Hermann 1976 – Bolivia, Yano 1981, 2011 – Brazil, Florschütz Waard 1990 – Guianas, Menzel 1992 – El Salvador, Moreno 1992a, b – Venezuela, Sharp *et al.* 1994 – Mexico, and Churchill & Linares 1995 – Colombia. For liverworts, these include Gradstein & Hekking 1989 – Guianas and Bolivia; Gradstein 2006 – French Guiana, Gradstein *et al.* 2007 – Ecuador, Gradstein 2016 – Colombia, Gradstein & León-Yáñez 2018 – Ecuador, Gradstein *et al.* 2018 – Colombia. But these provided primarily checklists and descriptions. Those publishing the lists of species often did not have access to specimens collected elsewhere. Hence, many species from multiple countries were named more than once, creating synonyms and inaccurate estimates of species numbers and distributions. It was not until keys became available that an ecologist had the tools needed to conduct ecological studies that included species information.

To illustrate the problems caused by synonyms among the bryophytes of the Neotropics, we need only examine a few studies. Delgadillo *et al.* (1995) indicated 4,103 species and varieties of mosses recorded from the

Neotropics. Within five years, subsequent taxonomic revisions reduced the number to 3,869 species and varieties (Delgadillo 2000). Only one year later, Gradstein *et al.* (2001, Table 2, page 3) estimated 3,980 species of all bryophytes in the Neotropics, including only 2,600 mosses, 1,350 liverworts, and 30 hornworts, based on systematic studies that found many synonyms.

Based on the 1996 expedition in the Chagos Archipelago (Neotropics; Figure 62), Seaward *et al.* (2006) found a good correlation of bryophyte diversity with island size. But only 19 taxa were recorded on the 25 islands (out of 55) that they explored. They attributed the low diversity to the remoteness and young age of the islands, as well as their small size. Nevertheless, where the bryophytes are found on these islands, they tend to be in abundance and play "significant" ecological roles. They found no evidence of host specificity of epiphytes and no epiphyllous species were found by the expedition.



Figure 62. Salomons Atoll in the Chagos Islands in the Indian Ocean. Photo by Charles and Anne Sheppard, through Creative Commons.

Bryophytes are advantageous as indicators of biodiversity and can be useful in broader conservation efforts in the Neotropics (Salazar Allen *et al.* 1996). Hence, the presentation of the treatise of Gradstein *et al.* (2001) is of tremendous value to all Neotropical bryophyte researchers. The two volumes present 200 genera of liverworts and 400 of mosses. They provide not only taxonomic aids, but also ecological attributes such as habitat indicators.

The rainforest of the Americas (**Neotropics**) is quite different from that in the African or Asian tropics (Gradstein & Pócs 1989). The New World Americas are characterized by **Pilotrichaceae** (Figure 63), **Phyllogoniaceae** (Figure 64), **Porotrichodendron** (Figure 65; **Lembophyllaceae**), **Chorisodontium** (Figure 66; **Dicranaceae**), **Octoblepharum** (Figure 67; lowland; **Octoblepharaceae**), and **Phyllodrepanium** (Figure 68; **Phyllodrepaniaceae**) among the mosses, and **Monocleaceae** (Figure 69) and numerous **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) among the liverworts. In the Asian **Lejeuneaceae**, the subfamily **Ptychanthoideae** (Figure 42) predominates, whereas in the Neotropics the **Brachiolejeuneae** (Figure 70-Figure 71) predominate (Gradstein 1991, 1994).



Figure 63. *Cyclodictyon* sp. (Pilotrichaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 66. *Chorisodontium mittenii*; *Chorisodontium* is a characteristic genus in the Neotropics. Photo by Jan-Peter Frahm, with permission.



Figure 64. *Phyllogonium viride* (Phyllogoniaceae), a genus characteristic of the Neotropics. Photo by Michael Lüth, with permission.



Figure 67. *Octoblepharum albidum*; *Octoblepharum* is a characteristic genus in the Neotropics. Photo by Niels Klazenga, with permission.



Figure 65. *Porotrichodendron superbum*, a characteristic species of the Neotropics. Photo by Juan David Parra, through Creative Commons.



Figure 68. *Phyllodrepanium falcifolium*, a moss characteristic of the Neotropics. Photo by Juan David Parra, through Creative Commons.



Figure 69. *Monoclea gottschei* (Monocleaceae), a thallose liverwort characteristic of the Neotropics, shown here with two sporophytes. Photo by Martin Nebel, courtesy of Robbert Gradstein.



Figure 70. *Dicranolejeunea axillaris* (Brachiolejeuneae) in abundance in the pampa of the Galapagos Islands. Photo courtesy of Robbert Gradstein.



Figure 71. *Lindigianthus cipaoneus* (Brachiolejeuneae) growing on tree fern in the Colombian Andes at 3000 m. Photo courtesy of Robbert Gradstein.

Nevertheless, disjunctions among the liverworts between the **Neotropics** (American tropics) and Africa are well known (Pócs 1976, 1992; Gradstein *et al.* 1983; Delgadillo 1993; Frahm 1995). Records in 1983 indicate 35 Afro-American shared species (see examples in Figure 72-Figure 73) (Gradstein *et al.* 1983). Most of these liverwort disjuncts are in the **Jungermanniales** (leafy liverworts) (Gradstein *et al.* 1983). By 1993, records indicated the Neotropics shared 334 bryophyte species and infraspecific taxa with the African tropics (Delgadillo 1993). This might be the result of an ancient land connection or long-distance dispersal. These are just hypotheses as experimental data on longevity of liverwort spores is greatly lacking (Gradstein *et al.* 1983). Another possibility is dispersal from Gondwanaland.

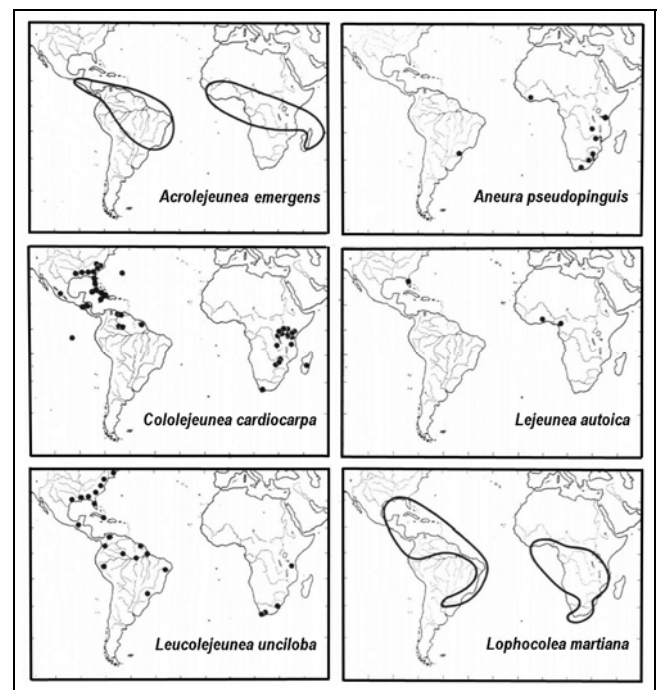


Figure 72. New and old tropical lowland disjunct species between Africa and the Americas. Modified from Gradstein *et al.* 1983.

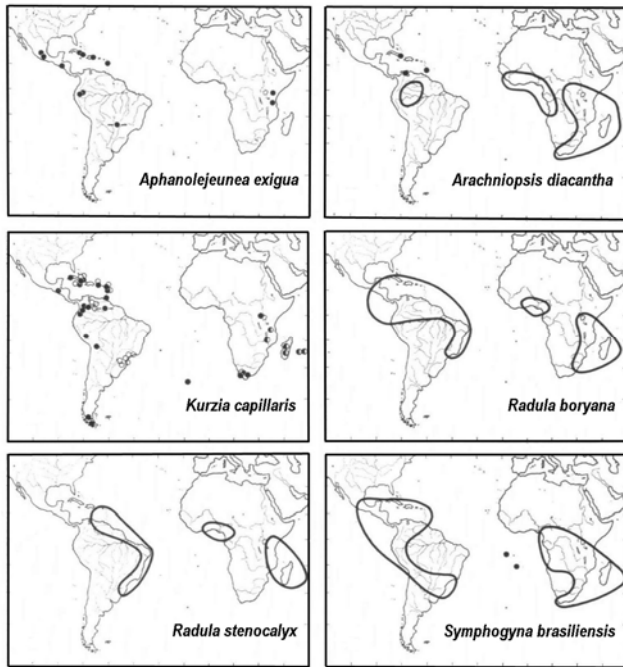


Figure 73. New and old tropical montane disjunct species between Africa and the Americas. Modified from Gradstein *et al.* 1983.

North and South America seem to have more species in common, sharing about 675 species (Delgadillo 1992, 1995). These include those with a continuous range and those with a disjunct distribution. Migration seems to have been stepwise, but some of these occurrences may have resulted from the breakup of previous distributions. Others arrived by long-distance dispersal. Other connections of the bryophyte flora to other parts of the Americas is through elevational distributions (Delgadillo & Cárdenas 1989). For example, the highlands of Chiapas, Mexico (Figure 74), are suitable for growth of species that may be found at lower elevations farther from the equator. The Chiapas have 155 taxa of mosses that fit into five phytogeographical elements. Mexico and Colombia alone share 371 moss species (Delgadillo 1992). Of these, 25 have a disjunct distribution that suggests long-distance dispersal. The Central American bridge facilitates the exchange of species, but the northern Andes in Colombia and the Neovolcanic Belt of Mexico form barriers that limit that exchange.

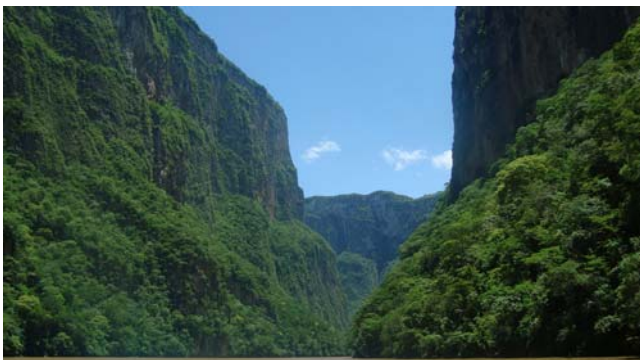


Figure 74. Sumidero Canyon, Chiapas, Mexico. Photo by Srplattano, through Creative Commons.

Delgadillo (1984) reported on mosses of the Mexican part of the Yucatan Peninsula (Figure 75). He identified 69 moss species and varieties and noted the similarities to the flora of the West Indies. There are virtually no endemics, perhaps due to the close connections with the Mexico mainland and the West Indies.



Figure 75. Yucatan moist forest, Mexico. Photo by Carlos Delgado, through Creative Commons.

In the *Liquidambar* forest (Figure 76) of Mexico, 194 species of mosses were known in 1979 (Delgadillo 1979). Of these, 70% are strictly American. This flora exhibits both a wide altitudinal and latitudinal range in Mexico and represents both tropical and temperate species.



Figure 76. *Liquidambar* forest canopy, through Creative Commons.

Herrera-Paniagua *et al.* (2008) reported 212 moss species for the Mexican state of Querétaro. As indicated by endemism, this state has three distinct regions: the conifer-cloud-temperate forests in the northeast (Sierra Madre Oriental), the more xeric parts in the center and southeast (Mexican Plateau and ecotone areas of the Transmexican Volcanic Belt), and the almost temperate areas in the south (Transmexican Volcanic Belt). The Sierra Madre Oriental province has the highest species richness.

It seems that almost any expedition even now is likely to reveal new records for the region. In 2001, Equihua *et al.* reported nine new moss records for Mexico from the Lacandona rainforest. The authors noted that these and other records continue to corroborate the continuity of bryophytes from North America to South America through the Central American bridge.

In a study of only 6 hectares (about 6 rugby fields or 10 American football fields) in a Costa Rican upper montane *Quercus* (oak) forest (Figure 77), Holz *et al.* (2002) found 100 species of mosses, 105 of liverworts, and 1 hornwort. In the oak forests and páramo of the Cordillera de Talamanca, Costa Rica, Holz and Gradstein (2005) found 401 species of bryophytes. In both studies, the number of mosses and liverworts was almost equal, with Holz and Gradstein finding 209 mosses, 191 liverworts, and 1 hornwort. To illustrate the limitations that early ground-based studies imposed, studies in the lowland rainforest found 50% of the bryophyte species only in the crowns and upper trunks, >10 m above the ground (Cornelissen & Gradstein 1990).



Figure 77. *Quercus* (oak) tropical montane forest. Photo by Cody Hinchliff, through Creative Commons.

Acebey *et al.* (2003) found similar high numbers of species in Bolivia (Figure 78). In a submontane rainforest there, they found 80 species on just six trees, 48 liverwort and 32 moss species. But they are quick to point out that finding nearly all the species in the forest requires only a small sample size. They estimate that these six trees had floras that represented 95% of the total bryophyte flora of the forest. Churchill *et al.* (2010) published a catalog of the bryophytes of Bolivia with discussions of diversity, distribution, and ecology.



Figure 78. Santa Cruz, Bolivia. Photo by Vincent Raalvia, through Creative Commons.

In Cuba (Figure 79), an island in the Greater Antilles, 383 taxa were reported, mainly from mountain areas (Motito *et al.* 1992). However, more recent studies seem to

be lacking, preventing an evaluation of Cuban species compared to those of other localities.



Figure 79. Montane moist forest on the slopes of Pico Turquino, Santiago de Cuba, Cuba. Photo by Male Gringo, through Creative Commons.

The tropical Andes (Figure 80) has by far the highest bryophyte diversity in the tropical Americas. For a general review on liverwort diversity in the Andes see Gradstein (1995b). Gradstein *et al.* (1977) compared oil body structures and examined the ecological distributions of selected species of the leafy liverworts in the Andes of Colombia. Churchill and co-workers listed 2,058 moss species names but suggested the actual number was probably closer to 1,500-1,700 because of likely synonyms (Churchill *et al.* 1995b).

The extraordinary biological richness of the Andean region is due to the great climatic and elevational variation of the area as well as historical factors. The authors concluded that an "increase in species diversity from the poles to the equator does not apply to mosses" (Churchill *et al.* 1995b). The latitudinal gradient has recently been studied by Shaw *et al.* (2005) for mosses and by Wang *et al.* (2016) for liverworts. These papers indicate that moss diversity is highest in the Southern Hemisphere and lowest in the Northern Hemisphere, with the tropics having an intermediate level. Liverwort diversity, in contrast, is highest in the tropics.



Figure 80. Andes, Ausangate hillside, Peru. Photo by Marturius, through Creative Commons.

An example of the high diversity is the San Francisco Biological Reserve in the Andes of southern Ecuador (Figure 81) (Gradstein *et al.* 2007). The reserve ranges from 1,800 to 3,100 m asl and consists of about 1,000 ha of pristine montane forest and páramo. Almost 570 species of bryophytes (357 liverworts, 206 mosses, 3 hornworts), including more than half the total number of liverwort species known from Ecuador, have been recorded from the reserve and the number is still rising (Schäfer-Verwimp *et al.* 2013; Gradstein & Benitez 2017). One reason for the high number of species recorded is probably the large number of bryologists who conducted fieldwork in the reserve and studied the collections. As Churchill *et al.* (2009) remarked: "One could readily predict similar diversity numbers throughout the montane forest of the tropical Andes employing such expertise. This study provides a basis for comparing other localities of similar vegetation and elevational range."



Figure 81. Reserva Biológica San Francisco, southern Ecuador. Photo courtesy of Robbert Gradstein.

In contrast, lowland habitats are usually less rich in bryophytes and do not provide for the same diversity seen by the rest of the flora and fauna (Churchill *et al.* 2009). While the number of niches in the multi-layered rainforest is relatively high, much of the tropical lowland is inhospitable to bryophytes, being too dry, too hot, or too dark. Whereas Churchill (1991) suggested that there is no strong latitudinal gradient of species richness from the temperate zone to the tropics, Hallingbäck (1992) further asserted that the temperate regions have a much higher diversity of mosses than is known in the tropics.

But "known" may be the operative word. On the one hand, many species have been described as different species multiple times; Ireland (1992) reduced the number of Latin American species of *Isopterygium* (Figure 82) from 92 to 8, Edwards (1980) accepted only 6 of the 93 species of *Calymperes* (Figure 83) from West Africa, and Bischler (1984) only 9 of 69 previously described New World *Marchantia* (Figure 3) species. Many taxa have been viewed as different simply because they were from a new place (O'Shea 2002). On the other hand, we are just beginning to explore the bryophytes high in the canopy through the use of a number of somewhat recent techniques (McClure 1966; Grison 1978; Perry 1978; Whitacre 1981; Parker *et al.* 1992; Gradstein 1996; Zotz & Vollrath 2003).

Cornelissen and Gradstein (1990) report that about 50% of the lowland rainforest bryophyte species of Guyana occur in the crowns and upper bole, typically missed by early bryological studies. Bryologists are beginning to find that the canopy of these primary forests may support many more species than the more-readily studied understory (Cornelissen & ter Steege 1989; Wolf 1993a, b). Bryophytes in the tropics find their dominance in different places from those in the temperate forests.



Figure 82. *Isopterygium tenerum*; the genus *Isopterygium* has had many of the same species named by different names in the tropics, creating many synonyms. Photo by John Bradford, with permission.



Figure 83. *Calymperes* sp. (Calymperaceae), one of the families that dominate in tropical Guyana. Photo by Niels Klazenga, with permission.

In the lowland rainforests of Mabura Hill, Guyana (Figure 84), South America, Cornelissen and Gradstein (1990) found 134 bryophyte species. The dominant bryophyte family is the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16), comprising about 30% of the cryptogamic flora (including bryophytes and lichens). As seems to be typical, the canopy accounted for 50% of the species. The humid mixed forest on loamy soil sports the richest liverwort flora.



Figure 84. Rainforest in Guyana. Photo through Creative Commons.

In Guyana (Figure 84), **Calymperaceae** (Figure 83), **Hookeriaceae** (Figure 133), **Hypnaceae** (Figure 85), **Orthotrichaceae** (Figure 112), and **Sematophyllaceae** (Figure 86) dominate the mosses. **Lepidoziaceae** (Figure 12), **Plagiochilaceae** (Figure 11), and **Frullaniaceae** (Figure 2, Figure 7-Figure 8), in addition to the species-rich **Lejeuneaceae** (Figure 6, Figure 15-Figure 16), are the predominant liverworts (Gradstein 1992). As will be discussed in another subchapter of this chapter, **epiphylls** (those algae, plants, and fungi living on leaves of other plants) are common in the lowland and lower montane rainforests.



Figure 85. *Mittenothamnium reptans*, in the family **Hypnaceae**, one of the dominant families from Guyana. Photo by Michael Lüth, with permission.

Montfoort and Ek (1990) have provided us with a detailed study in French Guiana (Figure 87), reporting 154 bryophyte species from only 28 mature trees (22 species) in a lowland rainforest by sampling from tree base to top of the canopy. Of these, 88 were liverworts, with 71 of these in the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16).



Figure 86. *Sematophyllum* sp. (**Sematophyllaceae**), one of the families that dominates in tropical Guyana. Photo by Michael Lüth, with permission.



Figure 87. Cataratas de Kaieteur, Guiana. Photo through Creative Commons.

In Kartabo, Co-operative Republic of Guiana (Figure 87), Graham (1933) also found the most diverse family to be the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). The most abundant moss here, by far, is *Rhaphidorrhynchium subsimplex* (see Figure 88), a species that is likewise abundant in Trinidad. Gradstein and Ilkiu-Borges (2009) compiled a guide to the liverworts and hornworts of Central French Guiana, including descriptions of habitats, especially the lowland cloud forest. This guide included 175 species of liverworts and 2 of hornworts, with the **Lejeuneaceae** again being the most species rich with 117 species. This guide recognized new combinations, providing updated nomenclature.



Figure 88. *Rhaphidorrhynchium callidum*; *R. subsimplex* is abundant in Kartabo in the Co-operative Republic of Guyana and in Trinidad. Photo by Juan Larrain, with permission.

In Moraballi Creek rainforest in the Co-operative Republic of Guyana (Figure 87), few species are very frequent (Richards 1954). *Calymperes lonchophyllum* (see Figure 89) and *Octoblepharum albidum* (Figure 90) occur in all synusiae (high canopy epiphytes, shade epiphytes, dead wood) except epiphyllous ones. Like most of the moist rainforests, the stream area is characterized by absence of ground-dwelling bryophytes, abundance of epiphyllous bryophytes, and dominance of the leafy liverwort family *Lejeuneaceae* (Figure 6, Figure 15-Figure 16).



Figure 89. *Calymperes tenerum* showing gemmae on leaf tips. *Calymperes lonchophyllum* is a frequent species, occurring in all synusiae except epiphylls at Moraballi Creek, Guyana. Photo by P. J. de Lange, through Creative Commons.



Figure 90. *Octoblepharum albidum*, a frequent species occurring in all synusiae except epiphylls at Moraballi Creek, Guyana. Photo by Janice Glime.

The Chocó region (Figure 91) of Colombia has the highest precipitation level in the Neotropical rainforests (Frahm 2012) and one of the wettest rainforests in the world (Frahm 1994), with an annual rainfall up to 12,000 mm, in some places even up to 15,000 mm. As a result, the bryophyte flora differs from elsewhere and the mosses do not serve as adequate indicators of the vegetational zones. Rather, this location permits us to observe the effects of high humidity on bryophytes.



Figure 91. Everwet lowland rainforest of the Chocó, Pacific coast of Colombia. Photo by Jan-Peter Frahm, with permission.

Frahm (1994, 2012) worked on the moss flora of the Chocó region. Although it has a high level of endemism in flowering plants, birds, and butterflies, the moss flora was

too poorly known to assess endemism. Frahm found 125 species of mosses on a transect from sea level to 1600 m elevation, using 10-hectare plots and different altitudes. In contrast, liverwort diversity in the same area was much higher, more than 200 species were reported, including 13 endemic taxa (Gradstein & Reiner-Drehwald 2017). In fact, Frahm (2012) found that mosses comprise only ~10% of the bryophyte cover, whereas elsewhere at the same elevational vegetation zone in the rainforest they comprise 40-50%. Gradstein (pers. comm.) commented that Frahm was able to finish his moss identifications quickly and get them published because there were rather few species only, whereas it took years to complete the many more liverwort identifications.

Some of the endemic liverworts of the Chocó region (Figure 91), such as *Fulfordianthus pterobryoides* (Figure 92), *Luteolejeunea herzogii*, and *Symbiezidium dentatum*, all members of *Lejeuneaceae* (Figure 6, Figure 15-Figure 16), are surprisingly common and widespread in the Chocó despite their absence elsewhere (Frahm 1994). The higher liverwort diversity in the Chocó is probably due to the exceedingly high humidity in the area.



Figure 92. The endemic *Fulfordianthus pterobryoides* on a twig in Chocó, Colombia. Photo by Jan-Peter Frahm, with permission.

When Vital and Visnadi (1994) surveyed the bryophyte flora of the Rio Branco Municipality in Brazil, they found only 76 species of bryophytes; 66 of these were new records for the State of Acre and 2 were new records for Brazil. The only hornwort was *Notothylas vitalii*

(Figure 93). We now know that there are at least 12 species of hornworts in Brazil (Felipe *et al.* 2016).



Figure 93. *Notothylas* sp.; *N. vitalii* was the only hornwort known to Vital and Visnadi from Rio Branco Municipality in Brazil in 1994. Photo by Blanka Aguero, with permission.

Costa (2003) studied the Amazonian rainforest bryophytes in Acre, Brazil. She revealed 514 species, with two field trips increasing the known bryoflora by 50%. She concluded that the diversity is still poorly known for the Brazilian Amazon.

In their study in the Chapada Diamantina region of Brazil, Valente *et al.* (2013) identified 400 bryophyte taxa, with the forests and **campos rupestres** (Figure 94; dry, rocky grasslands) accounting for 51% and 40%, respectively. The **caatinga** (Figure 95; shrub and thorn desert vegetation in interior northeastern Brazil) and **cerrado** (Figure 96; savanna) accounted for only 5% and 4%, respectively.



Figure 94. Campos Rupestres da Serra da Canastra, Brazil. Photo by Antonio José Maia Guimarães, through Creative Commons.



Figure 95. Caatinga – sertão nordestino, Brazil. Photo by Maria Hsu, through Creative Commons.



Figure 96. Cerrado, Campo Sujo, Brazil. Photo by Andreza Oliveira Borges, through Creative Commons.

Recent studies mostly support the earlier ones, but changes in nomenclature are reducing the numbers of endemic species. Costa and Peralta (2015) reported 1,524 species of bryophytes in Brazil, including 11 hornwort, 733 liverwort, and 880 moss species. As has been typical, the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) are the most abundant (285 species!). Following that record high are **Lepidoziaceae** (Figure 12) (48), **Frullaniaceae** (Figure 7-Figure 8) (37), **Ricciaceae** (Figure 54-Figure 55) (36), **Plagiochilaceae** (Figure 11) (27), **Radulaceae** (Figure 9-Figure 10) and **Metzgeriaceae** (Figure 13) (26 each), **Lophocoleaceae** (Figure 97) (18), **Aneuraceae** (Figure 14) (15), and **Calypogeiaceae** (Figure 98) (13). Surprisingly, **Sphagnaceae** (Figure 99) sets the record for mosses with 83 species, followed by **Fissidentaceae** (Figure 100) (65), **Pottiaceae** (Figure 101) (63), **Dicranaceae** (Figure 38, Figure 66) (54), **Bryaceae** (Figure 102) and **Sematophyllaceae** (Figure 86, Figure 135) (53 each), **Orthotrichaceae** (Figure 112) and **Pilotrichaceae** (Figure 103, Figure 133) (51 each), **Calymperaceae** (Figure 83, Figure 89) (48), and **Hypnaceae** (Figure 85) (28). Together, these account for 71% of the known bryophyte species in Brazil.



Figure 97. *Lophocolea cf. polychaeta* (**Lophocoleaceae**) from the Neotropics; **Lophocoleaceae** is one of the common liverwort families in Brazil. Photo by Michael Lüth, with permission.



Figure 98. *Calypogeia* (**Calypogeiaceae**) from the Neotropics; **Calypogeiaceae** is one of the common liverwort families in Brazil. Photo by Michael Lüth, with permission.



Figure 99. *Sphagnum cuspidatum* (**Sphagnaceae**); **Sphagnaceae** is the moss common moss family in Brazil. Photo by Michael Lüth, with permission.



Figure 100. *Fissidens asplenioides* (Fissidentaceae) from the Neotropics; Fissidentaceae is one of the common moss families in Brazil. Photo by Michael Lüth, with permission.



Figure 101. *Leptodontium stellatifolium* (Pottiaceae) from the Neotropics; Pottiaceae is one of the common moss families in Brazil. Photo by Michael Lüth, with permission.

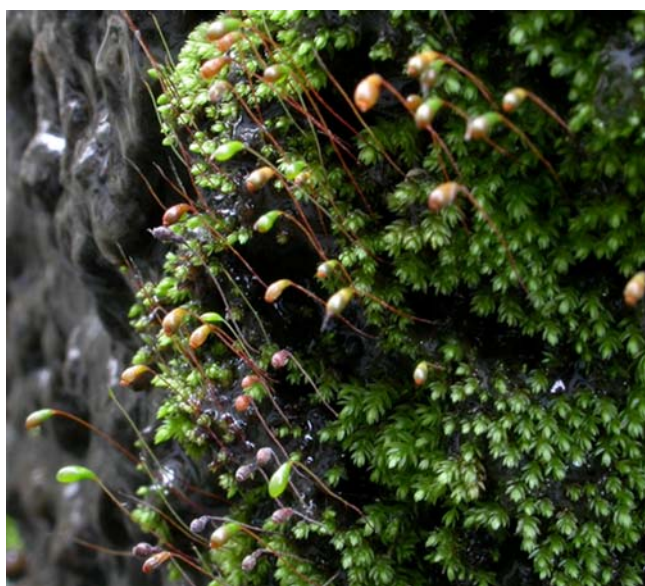


Figure 102. *Bryum cellulare* (Bryaceae); Bryaceae is one of the common moss families in Brazil. Photo by Li Zhang, with permission.



Figure 103. *Crossomitrium patrisiae* (Pilotrichaceae) from the Neotropics; Pilotrichaceae is one of the common moss families in Brazil. Photo by Michael Lüth, with permission.

Other new records include those of Oliveira and Alves (2007) for the State of Ceará, Brazil. Even at this recent date, 35 of the 81 species they identified were new for the state, and one was new for Brazil. In the Parque Ecológico de Gunma, Pará, Brazil, Fagundes *et al.* (2016) found 103 species, with the liverworts exhibiting the greater diversity (59). Of course the Lejeuneaceae again had the predominant representation of species (42). The rare species predominated with 62 species, whereas generalists were represented with only 47 species. Five new records were uncovered.

Oliveira and Bastos (2009) contributed to the knowledge of Anthocerotophyta and Marchantiophyta from Chapada da Ibiapaba, Ceará, Brazil. Of the 10 thallose liverwort species found, this study revealed 3 species of thallose liverworts for the first time in northeastern Brazil.

Florschütz-de Waard and Bekker (1987) compared the bryophyte flora in different forest types in West Suriname. They found the highest species richness in the marsh forest and the lowest in the savannah and xeromorphic (having structural adaptations to dry conditions) scrub forests. Based on their microclimatic data, they considered liverworts to have a greater ecological amplitude in these forests than that of mosses, a conclusion different from that in many ecosystems.

Although the Neotropics have not been studied to the degree of the temperate systems, most areas have had at least some studies. Spruce (1884-1885), Fulford (1963, 1966, 1968, 1976) and Gradstein (numerous papers, *e.g.* Liverwort Flora of Brazil by Gradstein & Costa 2003 and Liverwort Flora of French Guiana by Gradstein & Ilkiu-Borges 2009) studied liverworts. Very little work, however, has been done on the hornworts, a problem that Villarreal (2007) and others are attempting to rectify.

A number of additional general Neotropical floristic studies are available, but nomenclature should be reviewed to find more recent revisions: Delgadillo (1976) on bryophyte ecology in Veracruz, Mexico, Mägdefrau (1983 – forests and páramos of Venezuela and Colombia), van Reenen and Gradstein (1983, 1984), Timme (1985 – Peru), Buck & Thiers (1989), Gradstein *et al.* (1990 – Guianas, especially lowland forest), Richards (1991 – Co-operative

Republic of Guiana and West Indies), Sastre de Jesus & Santiago-Valentín [1996 – Puerto Rico, managed forests of *Cupressus* (Figure 25) and *Acacia* (Figure 26)], Churchill (1996 – Andes), Gradstein (1998 – páramos), Benavides *et al.* (2006) in the Colombian Amazon, Gradstein *et al.* (2016) on bryophytes of Sierra Nevada de Santa Marta, Colombia among others.

A few have ventured into ecological studies such as the vegetative variability of liverworts as demonstrated by *Bazzania* (Figure 104) (Bernecker 1990) or the differences among physiognomies in species richness and distribution (Valente *et al.* 2013). Others have sought to make broader statements regarding the ecology and biogeography (Gradstein & Pócs 1989). More recent studies, particularly on epiphytes, epiphylls, altitude, and rock outcrops, will be covered in more detail in subsequent subchapters of this chapter. These studies point to the need for more studies in order to gain a clear understanding of tropical bryophyte ecology.



Figure 104. *Bazzania* sp., a genus with vegetative variability from the Neotropics. Photo by Michael Lüth, with permission.

Endemism

Endemism (condition of species being unique to defined geographic location) has in the past been considered high in the tropics. In 1994 Delgadillo reported 48% endemism for mosses in the Neotropics. He suggested that endemism for mosses is higher in Bolivia, Costa Rica, and Ecuador than in other Neotropical areas. But he also considered that low numbers in some areas may be due to insufficient study. In others, low numbers result from strong connections with adjacent land masses having suitable habitat. I would also caution that high numbers may be the result of synonymy.

Frahm (2003) concluded that the rate of endemism is much higher in the tropics than outside the tropics but it is always much lower than that of tracheophytes (Table 2). Furthermore, we must consider these earlier numbers of endemics with skepticism. Throughout the tropics, many researchers worked independently of each other. They encountered bryophytes that were new to them and gave them new names. But researchers in other locations encountered these same bryophytes and gave them different names. There were no comprehensive keys to species from the tropics, and it was difficult to know that a species had

already been named by someone else in a different location.

Table 2. Percent of endemism in tracheophytes and bryophytes in tropical countries. From Frahm 2003.

	Tracheophytes	Bryophytes
Galapagos Islands	50%	10%
Cuba	50%	12%
Kilimanjaro		6%
Usambara Mtns.		3%
Réunion		9%
Mauritius		6%

Schuster (1982) explained the high degree of endemism in the liverwort flora of Gondwanaland (Figure 105) as a result of the break up and dispersal of Gondwanaland. The resulting isolation permitted speciation that led to endemism. This was further enhanced by extinctions in the Antarctic, leaving behind an isolated flora in New Zealand. Schuster attributes the current degree of endemism seen in the Antipodes (Australia and New Zealand) to the climate changes and breakup of Gondwanaland.



Figure 105. Gondwana Box Log Falls; Gondwanaland has a high degree of liverwort endemism. Photo by Malcolm Jacobson, through Creative Commons.

In Australia (Figure 60), endemism in the Wet Tropics is among the highest in the country (Stevenson *et al.* 2012). That area likewise had the highest number of species. Areas having high numbers of species were not necessarily the areas with endemism.

Schuster (1982) contended that only two areas had high levels of endemic genera: Australasia and South America. India (Figure 106) has few endemic groups, most likely reflecting wide-spread extinction of cool-adapted taxa. By contrast, Schuster listed 39 genera and 11 subgenera of leafy liverworts that were endemic to tropical America. All but two of these endemic genera are in the families **Acrobolbaceae** (Figure 107), **Cephaloziellaceae** (Figure 106, Figure 110-Figure 111), **Gymnomitriaceae** (Figure 108), **Jungermanniaceae** (Figure 109), and **Plagiochilaceae** (Figure 11), or the very specialized **Lejeuneaceae** (Figure 6, Figure 15-Figure 16). (Note that family classification may be different now.) The endemic species, furthermore, are usually highly specialized. One common feature of the liverwort genera *Pteropsiella* and *Protocephalozia* in the **Lepidoziaceae** (Figure 12) and *Phycolepidozia* (Figure 106, Figure 110-Figure 111) in the **Cephaloziellaceae** is that they develop either a thalloid or **confervoid** (loosely interwoven) gametophyte (Figure 111).



Figure 106. *Phycolepidozia indica* growing on rock in a forest fragment at Mt. Tandiamamol at 1600 m in the Western Ghats, India. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.



Figure 107. *Acrobolbus ciliatus*, in the **Acrobolbaceae**, a family with several endemic species in the Neotropics. Photo by Blanka Aguero, with permission.



Figure 108. *Gymnomitrium concinnatum*, in the **Gymnomitriaceae**, a family with several endemic species in the Neotropics. Photo by Herman Schachner, through Creative Commons.



Figure 109. *Jungermannia rubra* with perianth, in the family **Jungermanniaceae**, a family with a number of Neotropical endemic species. Photo by Ken-ichi Ueda, through Creative Commons.



Figure 110. *Phycolepidozia indica* habitat in forest fragments on Mt Tandiamamol, Western Ghats, at 1600 m. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.



Figure 111. *Phycolepidozia indica*, a species that can develop either a thalloid or **confervoid** (loosely interwoven) gametophyte. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.

In Australia (Figure 60), four endemic species of the moss *Macromitrium* (Figure 112) occur in higher elevation rainforests dominated by *Nothofagus moorei* (Figure 113) (Ramsay *et al.* 1987). The tropical rainforests have three endemic *Macromitrium* species: *M. peraristatum*, *M. dielsii*, and *M. funiforme*.



Figure 112. *Macromitrium ochraceum*, in a genus with four endemic species in Australia, three in the tropical rainforests there. Photo by Li Zhang, with permission.



Figure 113. *Nothofagus moorei* forest. Photo by David, through Creative Commons.

Karlin *et al.* (2012) used *Sphagnum palustre* (Figure 114) in Hawaii to explore the viability of a species from a single propagule. They concluded that this species currently has significant genetic diversity in Hawaii and that vegetative propagation does not preclude evolutionary success. This species is not known to produce sporophytes in Hawaii, although it does in other parts of the world (Figure 115).



Figure 114. *Sphagnum palustre*, a species with significant genetic diversity in Hawaii. Photo by Bernd Haynold, through Creative Commons.



Figure 115. *Sphagnum palustre* with capsules in Sweden. Photo by Oskar Gran, through Creative Commons.

Africa

In sub-Saharan Africa (Figure 116), O'Shea (1997b) reported 77% of the 3,000 taxa to be endemic. However, he warned that this figure may be misleading because the bryophyte flora of Africa was (and still is) so poorly known (and many may turn out to be synonyms).



Figure 116. Sub-Saharan Ruwenzori moss. Photo by Albert Backer, through Creative Commons.

Pócs (1998) found a high species diversity (~700 species known in 1998) along the Eastern Arc Mountains of Africa (Kenya and Tanzania; Figure 117), with only 32 (4.5%) endemic species, a low number even when compared to that of tracheophytes in the area.



Figure 117. Usambara Mountains, Eastern Arc Mountains, Tanzania. Photo by Joachim Huber, through Creative Commons.

Asia

In 2003, O'Shea reported 11% bryophyte endemism in Sri Lanka. The bryophyte flora of Sri Lanka is relatively rich, with 561 taxa. In fact, Gunawardene *et al.* (2007) considered the Western Ghats and Sri Lanka to be biodiversity hotspots.

In the Azores (Figure 118), of the 89 epiphyllous bryophyte species, 14 were considered endemic to the Azores or to Macaronesia (Sjögren 1997). These are somewhat frequent members of the endemic epiphyllous (Figure 119) association, the *Cololejeuneo-Colurion*: *Cololejeuneetum azoricae* (see Figure 48, Figure 119, Figure 120).



Figure 118. Island of Ponta Delgada, Azores. Photo by Laragheast, through public domain.

The Asian endemics of the **Ptychanthoideae** (Figure 42) in the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) tend to be restricted to subtropical and temperate regions, with the majority also known from Eocene fossils (Gradstein 1991). They are largely **relicts** (something that has survived from earlier period). The **Lejeuneoideae** (Figure 121-Figure 122) are mainly in the tropical

rainforests of the Malesian archipelago, are frequently highly specialized, and have no fossil records.



Figure 119. *Cololejeunea diaphana* and *Lejeunea floridana*, common epiphylls. Photo by Scott Zona, through Creative Commons.



Figure 120. *Colura leratii* in Fiji. Photo courtesy of Tamás Pócs.



Figure 121. *Lejeunea flava* (Lejeuneoideae) growing as an epiphyte. The **Lejeuneoideae** are common in tropical rainforests of the Malesian archipelago. Photo by Linda Phillips, through Creative Commons.



Figure 122. *Lejeunea flava* (Lejeuneoideae), growing as an epiphyll. Photo by Yang Jia-dong, through Creative Commons.

In 1987 Piippo *et al.* reported 48% endemism among the liverworts of New Guinea; 23% of the moss species seemed to be endemic. Most of these occur between 1500 and 3500 m elevation. The researchers found a high degree of endemism in the Frieda River Area and concluded that this is due to the high levels of metals in the area. The leafy liverworts *Bazzania* (Figure 104), *Frullania* (Figure 2, Figure 7-Figure 8), *Plagiochila* (Figure 11), and *Radula* (Figure 9-Figure 10) have a high degree of species endemism. The highest percentages of endemics among liverworts were in the **Plagiochilaceae** (Figure 11) (78%) and **Schistochilaceae** (Figure 123) (74%). Among the mosses, the number of species is much smaller, so the percentages may not be meaningful. The most notable may be the **Bryaceae** (Figure 124) with 35 species, 12 of which were considered endemic. The researchers cautioned that many of the families had not been studied well, so these numbers for both mosses and liverworts should be considered preliminary. All of these numbers will need revision after eliminating synonymy.



Figure 123. *Schistochila* sp., in the family **Schistochilaceae**, a family with many endemics in New Guinea. Photo by Li Zhang, with permission.



Figure 124. *Bryum billardieri*; *Bryum* is a genus with 12 endemic species in New Guinea. Photo by Jan-Peter Frahm, with permission.

Piippo (1994a) reported 38.2% endemism in Western Melanesia among the 440 species there. The highest reported endemism occurs in **Frullaniaceae** (Figure 2, Figure 7-Figure 8) and **Plagiochilaceae** (Figure 11). Although this is a slightly more recent study, synonyms again create a problem in determining endemism.

Piippo (1994b) also studied the liverwort family **Lejeuneaceae** (Figure 6, Figure 15-Figure 16) of Western Melanesia and reported that only 20.5% of these species were endemic. She attributed this to the large number of epiphyllous species in the family, a group that is widespread throughout the tropics.

Neotropics

Holz and Gradstein (2005) found more endemics in the oak (*Quercus*) forests of Central America than in the páramo. They considered that the high percentages of endemic bryophytes in oak forests in Central America reflected the importance of climatic changes associated with Pleistocene glaciations. In an older publication, Delgadillo (1998) likewise reported a high endemic element, with *ca.* 47% endemics. At that time, he reported 2,900 species of mosses, a number that decreases when systematic studies uncover synonymy. He considered isolation as the major contributor to endemism.

Delgadillo *et al.* (2003) compared endemism in the mosses, grasses, and Asteraceae. Of the 2,373 endemic taxa known among these groups, 86 are mosses; 2030 are Asteraceae. In an earlier study, Delgadillo and Cárdenas (2002) reported no endemic taxa from the Monies Azules Biosphere Reserve, where they identified 136 species and varieties, plus 8 more from published records.

Fortunately, there are now good Neotropical bryologists who are increasing our knowledge of that bryoflora. Costa *et al.* (2015) examined the species richness and floristic composition on an elevation gradient in the Itatiaia National Park in Brazil. They reported 519 taxa, representing 10 elevations, using literature, herbarium samples, and data banks. These represented 34% of the total Brazilian bryoflora.

In southeastern Brazil, the endemic *Bromeliophila natans* (Figure 125) is difficult to distinguish from *Lejeunea* (Figure 126) (Gradstein 1997). It was so-named because it lives in the basins of bromeliads (Figure 127) (Heinrichs *et al.* 2014). The Neotropical moss

Philophyllum tenuifolium (Leucomiaceae; Figure 128) is also restricted to this unusual habitat.

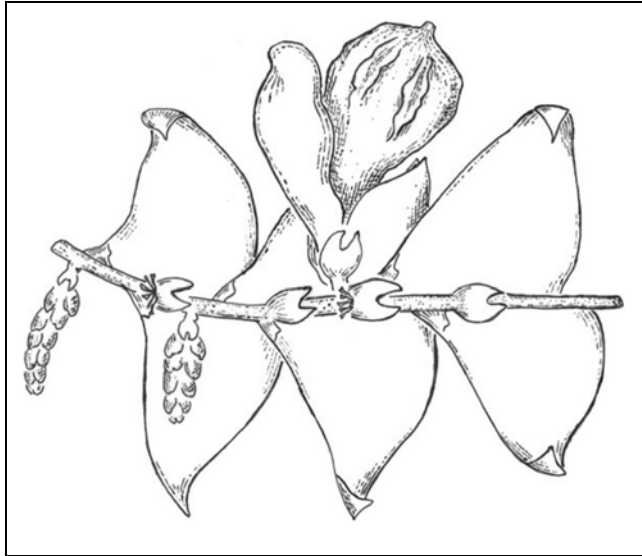


Figure 125. *Bromeliophila natans*, an endemic species that lives in bromeliad basins. Drawing from Heinrichs *et al.* 2014, slightly modified, through Robbert Gradstein.



Figure 126. *Lejeunea floridana* and *Cololejeunea cardiocarpa* on leaves. Photo by Scott Zona, with permission.



Figure 127. Bromeliads in the trees, showing basins where bryophytes can grow. Photo by Gail Hampshire, through Creative Commons.



Figure 128. *Philophyllum tenuifolium* herbarium specimen. Photo from Natural History Museum, London, through Creative Commons.

It is interesting that *Spruceanthus theobromae* (Figure 129) is endemic to the **Cacao** (source of cocoa) plantations (Figure 130) of western Ecuador (Gradstein 1999). Kautz and Gradstein (2001) concluded that because of its host specificity on **Cacao** and its exclusive occurrence in plantations, it should be removed from the World Red List of Bryophytes and its status changed to that of a near threatened species. Its survival depends on the low management intensity of plantations such as those in western Ecuador.



Figure 129. *Spruceanthus theobromae*, a species endemic to **Cacao** plantations in western Ecuador. Photo by Robbert Gradstein, with permission.



Figure 130. Cacao plantation in Cameroon. Photo by Barada-nikto, through Creative Commons.

Due to the efforts of a number of bryologists, the flora of Brazil is reasonably well known. Endemism in the Atlantic rainforest of Brazil reaches 242 endemic species out of the 1,337 species present (Costa & Peralta 2015). The dense ombrophilous forest here has 73% of these species represented, 62% of which are endemic. The southeastern region, with 1,228 species in total, has 219 endemic species. But the Atlantic rainforest in southeastern Brazil has most of the endangered species. Further monographic, worldwide or continent-wide studies may reduce the number of endemic species, but numbers are starting to approach reality.

Visnadi (2015) likewise reported on the Atlantic Forest of southeastern Brazil, at Mata Atlântica. This research revealed 199 species newly known for the area, bringing the total for the area to 220 species. This added two new records for Brazil and revealed locations of 13 Brazilian endemic species.

Causes of Endemism

Merckx *et al.* (2015) surmise that tropical mountains are diversity hot spots, but also exhibit a high degree of endemism. They point out that researchers have debated whether these mountain endemics originate more from local lowland taxa or from long-range dispersal from cool localities elsewhere. The latter could be similar to the separation of many frog species on different mountain tops, as discussed in the interaction chapter on amphibians in volume 2. This would presume that the species arrived, but was separated from interbreeding with the original species for a long enough period of time that a new species evolved. On the other hand, if the population originated from lower elevations, it might have become a new species through the **founder principle** (loss of genetic variation that occurs when new population is established by very small number of individuals from larger population), followed by natural selection for characters that suited their mountain habitat.

To try to answer this question, Merckx *et al.* (2015) examined the species on Mount Kinabalu, a 4,095 m high mountain in Sabah, East Malaysia. They found that most of the unique species of the mountain are younger than the mountain (6 million years). This mountain exhibits a mix of pre-adapted immigrant lineages and descendants from

local lowland ancestors, suggesting that the species did not arrive by long distance. Nevertheless, substantial shifts from lower to higher vegetation zones in these lowland groups were rare. The presence of sibling pairs of *Frullania* (Figure 2, Figure 7-Figure 8) with each member of the pair at a different elevation range of the same mountain (Figure 131) would tend to support the latter (Glime *et al.* 1990). Is there any reason to think that both processes could not occur? Is one of them the dominant cause?

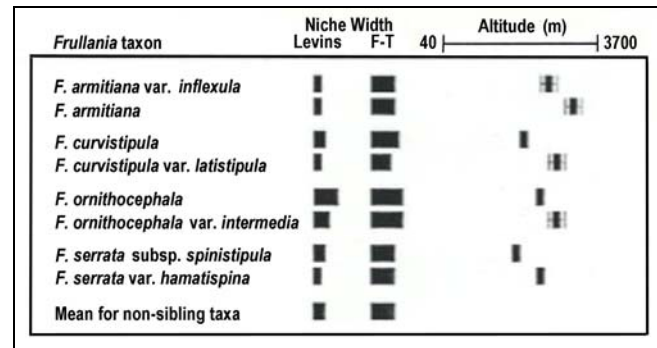


Figure 131. Levins and Freeman-Tukey niche width and elevational range of sibling pairs of *Frullania* on Mount Albert Edward, Papua New Guinea. Redrawn from Glime *et al.* 1990.

Patiño *et al.* (2014) attempted to explain the emergence of endemism by questioning why some genera diversify and others do not. Speciation on islands through gradual change from a founder population has been termed **anagenetic speciation**. They challenge this approach, saying that this process does not lead to "rapid and extensive speciation within lineages." Using surveys of the endemic bryophyte, fern, and seed plant floras of nine oceanic archipelagos, they showed that **anagenesis** (species formation without branching of evolutionary line of descent) was highest in bryophytes (73%), as measured by the proportion of genera with a single endemic species. Ferns had 65% and seed plants 55%. They concluded that "the dominance of anagenesis in island bryophytes and pteridophytes [ferns] is a result of a mixture of intrinsic factors, notably their strong preference for (sub)tropical forest environments, and extrinsic factors, including the long-term macro-ecological stability of these habitats and the associated strong phylogenetic niche conservatism of their floras."

Dangers to Endemics

Silva *et al.* (2014) raised concerns about conserving key species of bryophytes. They created potential distribution models for ten species that had been classified as bio-indicators of environmental quality and/or were endemic to the Atlantic Forest or to Brazil. Distributions of nine of the species could be explained by the Mean Diurnal Temperature Range. They raised concern that these species were not known in all the potentially suitable areas and that only 27% of the potentially suitable areas overlapped with Conservation Units. While these species were not specifically endemic, this approach could be used for determining the need for areas to protect endemic species.

Like Silva and coworkers (2014), Raxworthy *et al.* (2008) found that temperature was important in shifting altitudinal distributions of plants and animals, with

increasing temperature likely to surpass a warming threshold for some species. Of three endemic species in the tropical montane of Madagascar, two could not be relocated after 10 years. In addition, out of nine species analyzed, seven species had shifted their distributions to higher elevational means. In the 10 years of study, the mean lower elevation limit had shifted upward 29-114 m.

Tropical Rainforests

Whitmore (1998) provided an introduction to the tropical rainforest. These forests are evergreen, and the precipitation occurs more or less equally throughout the year, exceeding *ca.* 2000 mm per year. Under the umbrella of **rainforests** (Figure 132), Frahm and Gradstein (1991) recognized elevational rainforest types (see Chapter 8-1). The elevations of the different types of rain forest are lower on islands than on the continent. In areas with prolonged dry periods (>3 months), these forests are replaced with deciduous forests, seasonal forests, and savannahs. These types of forests will be discussed more specifically in the subchapters on Altitude.



Figure 132. Hawaiian tropical rainforest. Photo from Photoeverywhere, through Creative Commons.

Early researchers in the tropics considered the tropics to be an "inexhaustible" source of new bryophyte species (Pócs 1982). Richards (1954) bemoaned the scantiness of studies on the species and their ecology in tropical rainforests.

As one moves from the temperate zone into the tropics, there will be an increase in members of the moss families **Calymperaceae** (Figure 83, Figure 89) and **Sematophyllaceae** (Figure 86, Figure 135), in particular, as well as **Fissidentaceae** (Figure 17, Figure 41), **Leucobryaceae** (including *Octoblepharum*; Figure 67), **Pilotrichaceae** (Figure 133), and **Pterobryaceae** (Figure 134) (Pócs 1982). The **Calymperaceae** are distributed primarily in the humid lowland tropical and subtropical forests (Reese 1993). These primarily epiphytic taxa are usually dioicous but produce numerous gemmae at their leaf tips, facilitating short-distance dispersal (Gradstein & Pócs 1989). Whereas *Calymperes* (Figure 83) is restricted to the lowlands, another tropical member of **Calymperaceae**, *Syrrhopodon* (Figure 136), extends up to more than 2,000 m elevation. Both are primarily **corticulous** (growing on bark), but occur also on logs in the first stages of decomposition. In the **Sematophyllaceae**, *Taxithelium planum* (Figure 135) is abundant enough to

be termed a weed in the lowland tropical forests of the Americas (Buck 1985; Churchill & Salazar Allen 2001).



Figure 133. *Cyclodictyon* sp., representing **Pilotrichaceae**, a family that increases in representation as one goes toward the tropics. Photo by Michael Lüth, with permission.



Figure 134. *Pirella pohlii*, representing **Pterobryaceae**, a family that increases in numbers as one goes toward the tropics. Photo by Michael Lüth, with permission.



Figure 135. *Taxithelium planum*, a common moss species in lowland Neotropical forests. Photo by Michael Lüth, with permission.



Figure 136. *Syrrhopodon gaudichaudi* from the Neotropics, where the genus is known up to 2000 m asl. Photo by Michael Lüth, with permission.

Ramsay *et al.* (1987) stressed the importance of learning the role of bryophytes in the rainforest ecosystem in order to encourage more study of rainforest bryophytes. Jordan *et al.* (1980) could only hypothesize on the role of epiphytes in scavenging nutrients and moderating the flux of nutrients in the throughfall. Since then, Nadkarni and her students have greatly increased our knowledge of the role of bryophytes in nutrient relationships in the tropics (see Nutrient Relations in Chapter 8-1 of this volume).

Elevation and waterways are major contributors in determining the flora. Dixon (1935) described that below the Borneo ridgetop, cushions of the moss family **Dicranaceae** (Figure 38, Figure 66) are relatively common on both the ground and on logs, but liverworts remain more abundant. Near the stream, the large, pendent moss *Spiridens reinwardtii* (Figure 34) might be found on tall tree ferns. Dixon also reported abundant *Macromitrium ochraceum* (Figure 112) under the thin cover of *Dacrydium* (Figure 137; Podocarpaceae) and *Leptospermum* (Figure 138; Myrtaceae).



Figure 137. *Dacrydium cupressinum*; the genus *Dacrydium* provides cover for *Macromitrium ochraceum* near streams in Borneo. Photo by James Shook, through Creative Commons.



Figure 138. *Leptospermum trinervium*, in the genus that provides cover for *Macromitrium ochraceum* near streams in Borneo. Photo by John Tann, through Creative Commons.

Several additional studies are helpful in understanding the rainforest bryophyte communities. Giesenhagen (1910) described moss species of the rainforest. Pócs (1987) reported the changes in the biomass and productivity of bryophytes in east African rainforests. Gradstein and Pócs (1989) discussed tropical rainforest ecosystems and biogeography. Equihua and Gradstein (1995) compared the bryophyte communities of a rainforest with those of an old field. A more recent comprehensive study is that of Gradstein and Sporn (2010) on land use gradients.

Pantropical Distributions

Although liverworts seem to reach particularly high diversity in the tropics, moss richness estimates, based on 86 taxonomic checklists, do not support the hypothesis of a richer moss flora in the tropics compared to that of other latitudes (Shaw *et al.* 2005). Nevertheless, the latitudinal gradient for just North, Central, and South America was significant. Molecular data suggest that the Southern Hemisphere exhibits a higher diversity than does the Northern Hemisphere. The tropics are intermediate. Furthermore, virtually all the moss lineages are represented in all three latitudinal zones. Hence, it should be no surprise that mosses have travelled long distances and that many tropical mosses, particularly above the species level, are pantropical. This reasoning fits the Baas-Becking Hypothesis that everything is everywhere, a principle that seems to apply well to organism with small, resistant propagules such as spores (see Volume 2, Chapter 2-6; Pisa *et al.* 2013).

By examining tropical bryophyte communities in both Old World and New World tropics, Kürschner and Parolly (1999) could compare the differences. They concluded that although communities may be similar among the Americas, Africa, and Asia, there is not a **pantropical** (in tropics of both Eastern and Western Hemispheres) bryophyte flora. Could this be a result of too many bryologists giving different names to the same species in different places? In any case, there are clear similarities among the bryophyte communities of the three continents and a pantropical class of epiphyte communities can be recognized. Earlier, similarities and differences among the bryofloras of the tropical Americas, Africa, and Asia have been described by Theodor Herzog (1926) in his classical treatise *Geographie der Moose*. Recent studies such as that of Dauphin L. and Grayum (2005) support the relatively large number of

pantropical species, with 16% of their 55 collected species of bryophytes from the dry lowland forests and moist montane forests of the Santa Elena Peninsula and Islas Murciélago, Guanacaste Province, Costa Rica, being pantropical.

While most of the species are not pantropical, many families and genera are, and certain general community characters are present. For example, Germano and Pôrto (2006) examined bryophytes in Pernambuco, Brazil (Figure 139), and found that the community distribution patterns and growth forms were similar to those of other humid tropical forests, but in Pernambuco the richness was somewhat less. In their study, the most diverse bryophyte flora was that of **corticolous** (living on bark) bryophytes (33% of species). **Epixylic** (growing on wood, *i.e.*, trunks without bark, mostly logs) bryophytes were next (23%). With this high diversity, it is somewhat surprising that communities share 75% of the species. Liverwort diversity is higher than that of mosses, with a ratio of 23:1 among the **epiphyllous** (living on leaves) and 2:1 among corticolous species. However, **terricolous** (living on ground) species exhibited a 1:3 ratio of liverworts to mosses. The researchers also found that epixylic species were not specific for degree of decomposition, nor did richness vary with degree of decomposition.



Figure 139. National Park of Catimbau, Pernambuco, Brazil. Photo by Guilherme Jófili, through Creative Commons.

Pantropical bryophytes may represent convergent evolution under similar selection pressures, long-distance dispersal, or previous land bridges. Gradstein (2013) listed about 75 pantropical species of liverworts, and the number of pantropical mosses is probably similar. See Wołowski *et al.* (2014, pp. 176-177) for a list of pantropical species. Some pantropical species are notable.

Octoblepharum albidum (Figure 67) is a good example of a pantropical species and the most common of the **Leucobryaceae** (currently **Octoblepharaceae**), occurring on bark, tree bases, and early stages of log decomposition in lowlands and montane forests, up to more than 2,000 m (Churchill & Salazar Allen 2001). Its ability to reproduce vegetatively from easily broken leaf fragments, coupled with its monoicous condition resulting in numerous sporophytes, most likely contributes to its widespread and common pantropical presence.

Schofield and Crum (1972) summarized the theories on causes of disjunctions in bryophytes. These included continental drift, long-distance dispersal, and fragmentation of a formerly continuous distribution.

Substrate Specificity

Usable substrates in the understory of mature lowland forests are somewhat limited. The forest floor is typically covered with leaf litter that buries bryophytes. Rock surfaces may be available, especially vertical surfaces, if there is sufficient light. The forest itself provides trunk, branches, and leaf surfaces as substrates. At higher elevations, the soil and rock surfaces provide suitable surfaces. Soil in disturbed areas and other areas with sufficient light provides an available substrate. Bien (1982) examined substrate specificity of the leafy liverworts in a rainforest in Costa Rica. A later subchapter will be devoted to the leaf as a substrate for epiphyllous liverworts.

In a study in the Ecological Reserve of Gurjaú, Pernambuco, Brazil, Germano and Pôrto (2005) found few species that have substrate specificity. Rather, they typically occurred on two or three types of substrates. Some, however, were exclusively **corticolous** (bark-dwelling): ***Archilejeunea fuscescens*** (see Figure 140), ***Cheilolejeunea rigidula*** (see Figure 141), ***Lejeunea monimiae*** (Figure 142), some species of ***Frullania*** (Figure 2, Figure 7-Figure 8), and additional members of the **Lejeuneaceae** (Figure 6, Figure 15-Figure 16, Figure 142-Figure 143). Few epiphyllous species were restricted to leaves, including several species of ***Cololejeunea*** (Figure 119) and ***Leptolejeunea elliptica*** (Figure 143). Only ***Neckeropsis disticha*** (Figure 144) was restricted to rocks (**rupicolous**). On the ground the typical bryophytes were **Fissidentaceae** (Figure 17, Figure 41), thallose liverworts, and the hornwort ***Notothylas vitalii*** (see Figure 145).



Figure 140. ***Archilejeunea olivacea***; ***Archilejeunea fuscescens*** is a species that grows exclusively on bark at Pernambuco, Brazil. Photo by John Braggins, through Creative Commons.



Figure 141. *Cheilolejeunea imbricata*; *Cheilolejeunea rigidula* is a species that grows very commonly on bark at Pernambuco, Brazil. Photo by Yang Jia-dong, through Creative Commons.



Figure 144. *Neckeropsis undulata*, a family (Neckeraceae) that indicates very shady, wet habitats in the tropics. Photo by Michael Lüth, with permission.

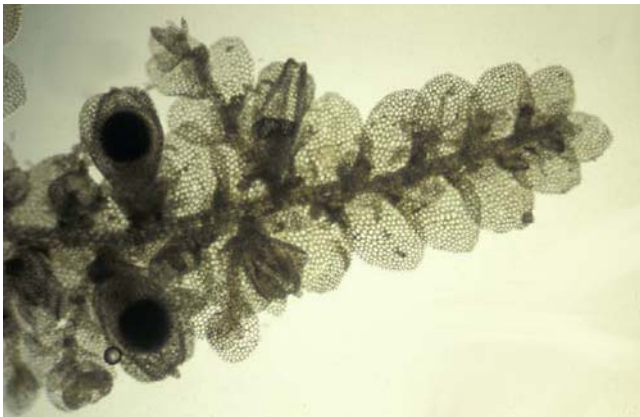


Figure 142. *Lejeunea monimiae*, a species that is strictly corticolous in the Pernambuco study site in Brazil. Photo by Elena Reiner-Drehwald, with permission.



Figure 145. *Notothylas javanica*; *N. vitalii* is a similar common hornwort on the ground in the Ecological Reserve of Gurjaú, Brazil. Photo by Li Zhang, with permission.



Figure 143. *Leptolejeunea elliptica*, a species restricted to leaves at the Pernambuco study site in Brazil. Photo by Yang Jia-dong through Creative Commons.

Forest Floor

The forest floor of the lowland rainforest is nearly devoid of bryophytes, suffering from the same leaf burial found in temperate deciduous forests (Richards 1954), but also suffering from the multi-layered canopy that blocks a large percentage of the sunlight.

But decaying logs, stumps, and branches here can host a number of taxa. It is here, in the low light and high humidity, that one finds *Leucobryum* (Figure 146) and mosses in the **Hookeriaceae** (Figure 133), **Hypnaceae** (Figure 85), and **Sematophyllaceae** (Figure 86, Figure 135) (Gradstein & Pócs 1989). Liverworts of the **Lepidoziaceae** and **Lophocoleaceae** (Figure 147), rather than the seemingly ever-present **Lejeuneaceae** (Figure 6, Figure 15-Figure 16, Figure 142-Figure 143), thrive here. Generally, only on road cuts, termite mounds, and other disturbed soil can one find bryophytes, including many *Fissidens* (Figure 17, Figure 41) species.



Figure 146. *Leucobryum juniperoideum*; *Leucobryum* occurs on stumps, logs, and branches in the tropics. Photo by Hermann Schachner, through Creative Commons.



Figure 147. *Leptoscyphus* sp., a tropical representative of the **Lophocoleaceae**, where the family is common on logs. Photo by Paul Davison, with permission.

Rock Houses

Outside the tropics, **rock houses** can mimic the conditions prevailing in some tropical habitats. These rockhouse cliffs, occurring as geologic formations in the eastern United States, are sufficiently deep holes among the rocks to buffer both temperature and moisture extremes. Added to this are very low light conditions, thus in several ways mimicking conditions deep under the tropical rainforest canopy. These caves house a group of endemic species whose closest relatives are tropical, as well as disjunct species with a primarily tropical range (Farrar 1998). Although the ferns are the most conspicuous of these plants, the bryophytes are the most numerous (Figure 148). Farrar suggests that their vegetative reproduction and adaptation to net photosynthetic gain in very low light makes their existence in these unusual habitats possible. Evidence of morphology, physiology, genetics, and geology suggest that they have persisted in these relict habitats since the pre-Pleistocene when the eastern U.S. experienced tropical and subtropical climates.



Figure 148. *Trichomanes petersii* and bryophytes. Rock houses have collections of plants similar to these. Photo by Robbin Moran, with permission through Dale Vitt.

Summary

Although some bryophytes are pantropical or have disjunct distributions on both sides of the Atlantic, their specialized habitats often restrict their distributions. This is indicated by a higher **beta diversity** among than within tropical regions. Nonetheless, the greatest number of bryophyte species occurs in the tropics. But many publications represent synonyms and many areas remain to be explored. Furthermore, it appears that increase in species diversity from the poles to the equator does not apply to mosses.

Tropical liverwort families are dominated by **Lejeuneaceae**, **Frullaniaceae**, **Radulaceae**, **Plagiochilaceae**, and **Lepidoziaceae**, with lesser numbers in **Metzgeriaceae** and **Aneuraceae**. The moss *Fissidens* has ~90 species in Africa. In tropical Asia, common mosses include the large species in **Dawsoniaceae**, **Garovagliaceae**, **Hypnodendraceae**, and **Spiridentaceae**. The liverwort family **Lejeuneaceae** is particularly species-rich in Asian tropics.

In the **Neotropics**, typical moss families are **Pilotrichaceae**, **Phyllogoniaceae**, **Lembophyllaceae**, **Dicranaceae**, **Octoblepharaceae**, and **Phylloandrepaniaceae**. Dominant liverwort families include **Monocleaceae** and **Lejeuneaceae**, with the subfamily **Ptychantheae** mainly in Asia and subfamily **Brachiolejeuneae** mainly in the Neotropics.

An inordinate number of endemic species has been reported from the tropics, but this number has been steadily decreasing as synonyms are determined. Furthermore, the rate of bryophytic endemism is much lower than that of tracheophytes. O'Shea reported that 77% of the sub-Saharan bryophyte flora was endemic, but warned that this large number probably represented many synonyms. Some of the liverwort families in Asia reach such high numbers, but mostly the endemism reported there is notably lower. Records are similar to those of Asia in the Neotropics. Tropical mountains are often diversity hot spots, and distance from similar habitats can lead to endemism, but these

also are a source of many synonyms. Nevertheless, differences in selection pressures with elevation can cause speciation. But endemic species, by their very nature of having a restricted distribution, increases their probability of extinction. Only 27% of the areas deemed suitable for them occur in protected areas.

The tropical rainforest provides a wide range of niches due to its multiple levels of vegetation heights. To the usual substrata of rocks, logs, trunks, and branches, the tree and shrub leaves add a highly diverse assemblage of liverworts. The soil, however, typically has too many leaves and not enough light penetration for bryophytes to survive. As one goes from the temperate zone to the tropics, the moss families **Calymperaceae**, **Sematophyllaceae**, **Fissidentaceae**, **Leucobryaceae/Octoblepharaceae**, **Pilotrichaceae**, and **Pterobryaceae** increase in representation. Liverworts are typically more species-rich than mosses.

In the eastern United States, rock houses created on mountainsides and slopes provide a tempered environment where a number of tropical species are able to survive.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make a very early version of this chapter reliable. Her helpful discussions kept me going on this part of the world I know so little about. S. Robbert Gradstein has been very helpful in discussions, obtaining images and references, and in providing a critical review of the chapter. Without his input this chapter would be far less complete. Tatiany Oliveira da Silva provided a critical reading for clarity, provided additional references, and shared her knowledge of the Amazon.

Literature Cited

- Acebey, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.
- Adebisi, A. O. and Oyeyemi, S. D. 2013. Distribution of mosses in Ekiti State, Nigeria. *N. Y. Sci. J.* 6: 23-25.
- Ah-Peng, C., Bardat, J., Stamenoff, P., Hedderson, T. A., and Strasberg, D. 2010. Bryophytes of the island of La Réunion: Diversity, endemism and conservation. *Cryptog. Bryol.* 31: 241-270.
- Akiyama, H., Yamaguchi, T., and Suleiman, M. 2001. The bryophyte flora of Kinabalu National Park (Sabah, Malaysia), based on the collections by Japan-Malaysia collaborative expeditions in 1997. *Nat. Human Activ.* 6: 83-99.
- Allen, B. H. 1987. A revision of the genus *Leucomium* (Leucomiaceae). *Mem. N. Y. Bot. Gard.* 45: 661-677.
- Arnell, S. 1956. Hepaticae collected by O. Hedberg *et al.* on the East African Mountains. *Arkiv Bot.* 3: 517-562.
- Benavides, J. C., Duque M., A. J., Duivenvoorden, J. F., and Cleef, A. M. 2006. Species richness and distribution of understorey bryophytes in different forest types in Colombian Amazonia. *J. Bryol.* 28: 182-189.
- Berghen, C. vanden. 1983. *Lepidozia* Dum. emend. Joerg. subgen. *Sprucella* (Steph.) Vanden Berghen comb. et stat. nov. (Hepaticae). *Bull. Jard. Bot. Nat. Belg.* 53: 321-330.
- Bernecker, A. 1990. Zur Variabilität vegetativer Merkmale tropischer Lebermoose am Beispiel der Gattung *Bazzania* S. F. Gray. [On the variability of vegetative features of tropical liverworts using the example of the genus *Bazzania* S. F. Gray.] M. Sc. Thesis, University of Ulm, Germany.
- Bien, A. 1982. Substrate specificity of leafy liverworts (Hepaticae: Lejeuneaceae) in a Costa Rican rainforest. M.Sc. Thesis, State University of New York, Suny Brook.
- Bischler, H. 1984. *Marchantia* L. The New World species. *Bryophyt. Biblio.* 26: 1-228.
- Bizot, M. and Pócs, T. 1974. East African bryophytes, I. *Acta Acad. Paed. Agriensis nov. ser.* 12: 383-449.
- Bizot, M. and Pócs, T. 1979. East African bryophytes, III. *Acta Bot. Acad. Sci. Hung.* 25: 223-261.
- Bizot, M. and Pócs, T. 1982. East African bryophytes, V. *Acta Bot. Acad. Sci. Hung.* 28: 15-64.
- Bowers, F. D. 1974. The mosses reported from Costa Rica. *Bryologist* 77: 150-171.
- Bruggeman-Nannenga, M. A. 2013a. *Fissidens tamaspocsi* and *F. magnicellulatus* spp. nov. from eastern Africa and validation of *F. cyatheicola*. *Lindbergia* 36: 9-16.
- Bruggeman-Nannenga, M. A. 2013b. Two new *Fissidens* species (Fissidentaceae) from Tropical East Africa and *Fissidens bessouensis* Corb., a remarkable species with fimbriate leaves and multicellular spores. *Polish Bot. J.* 58: 117-125.
- Buck, W. R. 1985. A review of *Taxithelium* (Sematophyllaceae) in Brazil. *Acta Amazonica Suppl.* 15: 43-53.
- Buck, W. R. and Thiers, B. M. 1989. Review of bryological studies in the tropics. In: Campbell, D. G. and Hammond, H. D. (eds.). *Floristic inventory of tropical countries*. New York Botanical Garden, Bronx, N. Y., pp. 484-493.
- Chuah-Petiot, M. 2011. A checklist of Hepaticae and Anthocerotae of Malaysia. *Polish Bot. J.* 56: 1-44.
- Churchill, S. P. 1991. The floristic composition and elevational distribution of Colombian mosses. *Bryologist* 94: 157-167.
- Churchill, S. P. 1996. Andean moss diversity and conservation: State of knowledge and prerequisites for the future. *An. Inst. Biol. Univ. Nac. Auton. Mexico* 67: 169-176.
- Churchill, S. P. and Linares, E. L. 1995. *Prodromus Bryologiae Novo-Granatensis*. 2 vols. Bogotá.
- Churchill, S. P. and Salazar Allen, N. 2001. Mosses. In: Gradstein, S. R., Churchill, S. P., and Salazar Allen, N. *Guide to the Bryophytes of Tropical America*. *Mem. N. Y. Bot. Gard.* 86: 240-571.
- Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. 1995a. Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden, Bronx, N. Y., 702 pp.
- Churchill, S. P., Griffin, D. III, and Lewis, M. 1995b. Moss diversity of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, New York, N. Y., pp. 335-346.
- Churchill, S. P., Neill, D., Jaramillo C., E., and Quizhpe, W. 2009. Bryophytes from the Cordillera del Condór, Ecuador. *Trop. Bryol.* 30: 92-101.
- Churchill, S. P., Sanjines A., N. N., and Aldana M., C. 2010. Catálogo de las briofitas de Bolivia: Diversidad, distribución y ecología. Missouri Botanical Garden, 340 pp.
- Cornelissen, J. H. C. and Gradstein, S. R. 1990. On the occurrence of bryophytes and macrolichens in different

- lowland rain forest types at Mabura Hill, Guyana. *Trop. Bryol.* 3: 29-35.
- Cornelissen, J. H. C. and Steege, H. ter. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.
- Costa, D. P. 2003. Floristic composition and diversity of Amazonian rainforest bryophytes in the state of Acre, Brazil. *Acta Amazon.* 33: 399-414.
- Costa, D. P. and Peralta, D. F. 2015. Bryophytes diversity in Brazil. *Rodriguésia* 66: 1063-1071.
- Costa, D. P., Santos, N. D., Rezende, M. A., Buck, W. R., and Schäfer-Verwimp, A. 2015. Bryoflora of the Itatiaia National Park along an elevation gradient: Diversity and conservation. *Biodiv. Conserv.* 24: 2199-2212.
- Crum, H. 1983. Mosses of the Great Lakes Forest. University Herbarium, University of Michigan, Ann Arbor, Michigan, p. 66.
- Dauphin L., G. and Grayum, M. H. 2005. Bryophytes of the Santa Elena Peninsula and Islas Murciélago, Guanacaste, Costa Rica, with special attention to Neotropical dry forest habitats. *Lankesteriana* 5(1): 53-61.
- Delgadillo M., C. 1976. Estudio botánico y ecológico de la región de Río Uxpanapa, Veracruz. No. 3. Los Musgos. *Publ. Inst. Invest. Recurs. Bioticos* 1: 19-28.
- Delgadillo M., C. 1979. Mosses and phytogeography of the Liquidambar forest of Mexico. *Bryologist* 82: 432-449.
- Delgadillo M., C. 1984. Mosses of the Yucatan Peninsula, Mexico. III. Phytogeography. *Bryologist* 87: 12-16..
- Delgadillo M., C. 1992. Moss interchange: Bryofloristic similarities between Mexico and Colombia and the phytogeographical role of the Central American bridge. *Bryologist* 95: 261-265.
- Delgadillo M., C. 1993. The Neotropical-African disjunction. *Bryologist* 96: 604-615.
- Delgadillo M., C. 1994. Endemism in the Neotropical moss flora. *Biotropica* 26: 12-16.
- Delgadillo M., C. 1995. Neotropical moss floras: Species common to North and South America. *Trop. Bryol.* 10: 1-6.
- Delgadillo M., C. 1998. Los musgos, la diversidad y sus causas en el Neotrópico. [Mosses, diversity and their causes in the Neotropics.]. *Monogr. Syst. Bot. (Missouri Botanical Garden)* 68: 61-67.
- Delgadillo M., C. 2000. Distribución geográfica y diversidad de los musgos neotropicales. *Bol. Soc. Bot. México* 65: 63-70.
- Delgadillo M., C. and Cárdenas S., A. 1989. Phytogeography of high-elevation mosses from Chiapas, Mexico. *Bryologist* 92: 461-466.
- Delgadillo M., C. and Cárdenas S., Á. 2002. The Lacandon Forest (Chiapas, Mexico): A benchmark area for tropical mosses. *Bryologist* 105: 327-333.
- Delgadillo M., C., Bello, B., and Cárdenas, A. 1995. Latmoss: A catalogue of Neotropical mosses. *Missouri Botanical Garden, St. Louis*, pp. 1-191.
- Delgadillo M., C., Ríos, J. L. V., and Aranda, P. D. 2003. Endemism in the Mexican flora: A comparative study in three plant groups. *Ann. Missouri Bot. Gard.* 90: 25-34.
- Dixon, H. N. 1935. A contribution to the moss flora of Borneo. *J. Linn. Soc. Bot.* 50: 60-65.
- Dong, S., Schäfer-Verwimp, A., Meinecke, P., Feldberg, K., Bombosch, A., Pócs, T., Schmidt, A. R., Reitner, J., Schneider, H., and Heinrichs, J. 2012. Tramps, narrow endemics and morphologically cryptic species in the epiphyllous liverwort *Diplasiolejeunea*. *Molec. Phylogen. Evol.* 65: 582-594.
- Edwards, S. R. 1980. A revision of west tropical African Calymperaceae I. Introduction and Calymperes. *J. Bryol.* 11: 49-93.
- Equihua, C. and Gradstein, S. R. 1995. Bryofloristic comparison between an old field and a rain forest: Preliminary results. *Tropical Bryophytes: Biology, Diversity and Conservation. Abstracts.* Mexico City.
- Equihua, C., Newton, A. E., García-Ávila, D., De Luna, E., and Gradstein, S. R. 2001. New moss records for Mexico from the Lacandona tropical rain forest, Chiapas. *Bryologist* 104: 602-606.
- Ezukanma, I. O., Ogundipe, O. T., Nodza, G. I., and Pócs, T. 2017. Bryophyte records from the Eastern Nigerian Highlands. *Polish Bot. J.* 62: 203-212.
- Fagundes, D., Tavares-Martins, A. C., Ilkiu-Borges, A. L., Moraes, N. R., and Santos, R. C. 2016. Riqueza e aspectos ecológicos das comunidades de briófitas (Bryophyta e Marchantiophyta) de um fragmento de Floresta de Terra Firme no Parque Ecológico de Gunma, Pará, Brasil. *Iheringia, Série Botânica* 71: 72-84.
- Farrar, D. R. 1998. The tropical flora of rockhouse cliff formations in the eastern United States. *J. Torrey Bot. Soc.* 125(2): 91-108.
- Felipe, G., Bojacá, P., Maciel-Silva, A. S., Oliveira, B. A., Araújo, C. A. T., Fantecelle, L. B., and Villarreal, J. C. 2016. Flora do Brasil 2020 Anthocerotophyta. *Compilação monográfica das espécies de antóceros registradas no Brasil, Flora do Brasil 2020.* Accessed 25 October 2018 at <adaisesmaciel.wixsite.com/briofitasufing>, 40 pp.
- Fischer, E. 2013. Liverworts and Hornworts of Rwanda. *Abc Taxa Vol 14*: 552 pp.
- Florschütz-de Waard, J. 1990. A catalogue of the bryophytes of the Guianas. II. Musci. *Trop. Bryol.* 3: 89-104.
- Florschütz-de Waard, J. and Bekker, J. M. 1987. A comparative study of the bryophyte flora of different forest types in West Suriname. *Cryptog. Bryol. Lichénol.* 8: 31-45.
- Frahm, J.-P. 1994. A contribution to the bryoflora of the Chocó region, Colombia. I. Mosses. *Trop. Bryol.* 9: 89-110.
- Frahm, J.-P. 1995. Correlations between the European, tropical African, and tropical American moss floras. *Frag. Flor. Geobot.* 40: 235-250.
- Frahm, J.-P. 2003. *Manual of Tropical Bryology.* *Trop. Bryol.* 23: 1-196.
- Frahm, J.-P. 2012. Mosses and liverworts of the Chocó region. *Arch. Bryol.* 123: 1-14.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Frahm, J.-P., Frey, W., Kurschner, H., and Menzel, M. 1990. Mosses and liverworts of Mt. Kinabalu. *Sabah Parks Publication* 12: 1-91.
- Frahm, J. P., Pócs, T., O'Shea, B., Koponen, T., Piipo, S., Enroth, J., Rao, P.-C., and Fang, Y. 2003. *Manual of tropical bryology.* *Trop. Bryol.* 23: 1-200.
- Fulford, M. H. 1963. *Manual of the leafy Hepaticae of Latin America I.* *Mem. N. Y. Bot. Gard.* 11: 1-172.
- Fulford, M. H. 1966. *Manual of the leafy Hepaticae of Latin America II.* *Mem. N. Y. Bot. Gard.* 11: 173-276.
- Fulford, M. H. 1968. *Manual of the leafy Hepaticae of Latin America III.* *Mem. N. Y. Bot. Gard.* 11: 277-392.
- Fulford, M. H. 1976. *Manual of the leafy Hepaticae of Latin America IV.* *Mem. N. Y. Bot. Gard.* 11: 393-535.

- Germano, S. R. and Pôrto, K. C. 2005. A bryophyte checklist of the Ecological Reserve of Gurjaú, Pernambuco, Brazil. *Trop. Bryol.* 26: 1-12.
- Germano, S. R. and Pôrto, K. C. 2006. Bryophyte communities in an Atlantic forest remnant, state of Pernambuco, Brazil. *Cryptog. Bryol.* 27: 153-163.
- Giesenhagen, K. 1910. Die Moostypen de Regenwälder. [The moss types of rainforests.]. *Ann. Jard. Bot. Buitenz.* (suppl. 3, pt.2): 711-790.
- Glime, J. M., Hudy, P. S., and Hattori, S. 1990. Diversity and altitudinal niche width characteristics for 35 taxa of the Papua New Guinea *Frullania* flora with consideration of sibling pairs. *Trop. Bryol.* 2: 103-117.
- Gradstein, S. R. 1991. Diversity and distribution of Asian Lejeuneaceae subfamily Ptychanthoideae. *Trop. Bryol.* 4: 1-16.
- Gradstein, S. R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 234-258.
- Gradstein, S. R. 1994. Lejeuneaceae: Ptychantheae, Brachiolejeuneae. *Flora Neotrop.* 62: 1-216.
- Gradstein, S. R. 1995a. Bryophyte diversity of the tropical rainforest. *Archs. Sci. Genève* 48: 91-96.
- Gradstein, S. R. 1995b. Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, Bronx, N. Y., pp. 321-334.
- Gradstein, S. R. 1996. Corticolous bryophytes. *Ecotropica* 2: 63-65.
- Gradstein, S. R. 1997. *Bromeliophila helenae*, a new species of Lejeuneaceae from the Neotropics. *Cryptog. Bryol. Lichénol.* 18: 217-221.
- Gradstein, S. R. 1998. Hepatic diversity in the Neotropical páramos. *Monogr. Syst. Bot. (Missouri Botanical Garden)* 68: 69-85.
- Gradstein, S. R. 1999. On the rediscovery of *Spruceanthus theobromae* (Lejeuneaceae, Hepaticae), an endangered species on cacao trees in western Ecuador. *Bryobrothera* 5: 81-86.
- Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. *Cryptog. Bryol.* 27: 141-152.
- Gradstein, S. R. 2011. Guide to the Liverworts and Hornworts of Java. Seameo-Biotrop Scientific Publications, Bogor, Indonesia, 150 pp.
- Gradstein, S. R. 2013. Afro-American hepatics revisited. *Polish Bot. J.* 58: 149-177.
- Gradstein, S. R. 2016. A new key to the genera of liverworts of Colombia. [Nueva clave para los géneros de Hepáticas de Colombia.]. *Caldasia* 38: 225-249.
- Gradstein, S. R. and Benitez, A. 2017. Liverworts new to Ecuador with description of *Plagiochila priceana* sp. nov. and *Syzygiella burghardtii* sp. nov. *Cryptog. Bryol.* 38: 335-348.
- Gradstein, S. R. and Costa, D. P. 2003. The Liverworts and Hornworts of Brazil. *Mem. N. Y. Bot. Gard.* 87: 1-317.
- Gradstein, S. R. and Hekking, W. H. A. 1989. A catalogue of the bryophytes of the Guianas. I. Hepaticae and Anthocerotae. *J. Hattori Bot. Lab.* 66: 197-230.
- Gradstein, S. R. and Ilkiu-Borges, A. L. 2009. Guide to the Vascular Plants of Central French Guiana. Part 4. Liverworts and Hornworts. *Mem. N. Y. Bot. Gard.* 76(4): 140 pp.
- Gradstein, S. R. and León-Yáñez, S. 2018. Liverworts (Marchantiophyta) of *Polylepis pautae* forests from Ecuador with description of *Leptoscyphus leoniae* sp. nov. and *Plagiochila pautaphila* sp. nov. *Nova Hedw.* 106: 35-48.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World*. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies. Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R. and Reiner-Drehwald, M. E. 2017. A new species of *Cyclolejeunea* (Marchantiophyta: Lejeuneaceae) from the Chocó, Colombia. *Bryo. Divers. Evol.* 39: 21-27.
- Gradstein, S. R. and Sporn, S. G. 2010. Diversity of epiphytic bryophytes along land use gradients in the tropics. *Nova Hedw. Beih.* 138: 309-321.
- Gradstein, S. R., Cleef, S. R., and Fulford, M. H. 1977. Hepaticae oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. *Studies on Colombian Cryptograms*. Koninklijke Nederlandse Academie van Wetenschappen, Prof. Series C, 80: 377-420.
- Gradstein, S. R., Pócs, T., and Vána, J. 1983. Disjunct Hepaticae in tropical America and Africa. *Acta Bot. Hung.* 29: 127-171.
- Gradstein, S. R., Montfoort, D., and Cornelissen, J. H. C. 1990. Species richness and phytogeography of the bryophyte flora of the Guianas, with special reference to the lowland forest. *Trop. Bryol.* 2: 117-126.
- Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001. Guide to the Bryophytes of Tropical America. *Mem. N. Y. Bot. Gard.* 86: 1-577.
- Gradstein, S. R., Tan, B. C., Zhu, R.-L., Ho, B.-C., King, C. S.-H., Drübert, C., and Pitopang, R. 2005. A catalogue of the bryophytes of Sulawesi, Indonesia. *J. Hattori Bot. Lab.* 98: 213-257.
- Gradstein, S. R., Bock, C., Mandl, N., and Nöske, N. M. 2007. 04A Bryophyta: Liverworts and Hornworts. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S. Ecuador). *Ecotropica*. Monogr. 4: 69-87.
- Gradstein, S. R., Morales, C., Negritto, M. A., and Duckett, J. G. 2016. New records of liverworts and hornworts from the Sierra Nevada de Santa Marta, Colombia. *Cryptog. Bryol.* 37: 463-475.
- Gradstein, S. R., Uribe-M., J., Gil-N., J. E., Morales, C., and Negritto, M. A. 2018. Liverworts new to Colombia. *Caldasia*, 40: 82-90.
- Graham, E. H. 1933. Bryophytes of the Kartabo Region, British Guiana. *Bryologist* 36: 59-67.
- Grisson, F. 1978. Amélioration génétique de L'Okoumé. Bois et Forêts de Tropiques 179: 3-26.
- Grolle, R. 1993. Taxonomic Results of the BRYOTROP Expedition to Zaire and Rwanda 9. Pallaviciniaceae, Haplomitriaceae. *Trop. Bryol.* 8: 75-82.
- Gunawardene, N. R., Daniels, D. A., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., Karunakaran, P. V., Nayak, G. K., Prasad, S., Puyravaud, P., Ramesh, B. R., Subramanian, K. A., and Vasanthy, G. 2007. A brief overview of the Western Ghats-Sri Lanka biodiversity hotspot. *Curr. Sci.* 93: 1567-1572.
- Hallingbäck, T. 1992. Sveriges boreala mossflora i ett internationellt perspektiv. [The boreal bryophyte flora of Sweden in an international perspective.]. *Svensk Bot. Tidskr.* 68: 177-184.

- Hedderson, T. A., Gwynne-Evans, D., Ah-Peng, C., and Ribeiro, D. 2015. A contribution to the bryoflora of Mozambique from the 'Google Forest,' Mabu Mountain, Zambezia Province. *J. Bryol.* 37: 42-48.
- Hedenäs, L. 2007. Global diversity patterns among pleurocarpous mosses. *Bryologist* 110: 319-331.
- Heinrichs, J., Czumaj, A., Dong, S., Scheben, A., Schäfer-Verwimp, A., Peralta, D. F., Kathrin Feldberg, K., Schmidt, A. R., and Schneider, H. 2014. The Bromeliaceae tank dweller *Bromeliophila* (Lejeuneaceae, Porellales) is a member of the *Cyclolejeunea-Prionolejeunea* clade. *Plant Syst. Evol.* 300: 63-73.
- Hermann, F. J. 1976. Recopilacion de los musgos de Bolivia. *Bryologist* 79: 123-171.
- Herrera-Paniagua, P., Delgadillo M., C., Ríos, J. L. V., and Luna-Vega, I. 2008. Floristics and biogeography of the mosses of the state of Querétaro, Mexico. *Bryologist* 111: 41-56.
- Herzog, T. 1926. *Geographie der Moose*. Fischer, Jena.
- Higuchi, M. and Lin, S.-H. 2005. *Takakia lepidiozoides* S. Hatt. & Inoue (Musc.) new to Taiwan. *Bryol. Res.* 8: 349-352.
- Higuchi, M., Arikawa, T., and Suleiman, M. 2008. Mosses of Mt. Kinabalu, Borneo, Malaysia. *Mem. Natl. Mus. Nat. Sci.* 45: 93-104.
- Hodgetts, N. G., Essilfie, M. K., Adu-Gyamfi, A., Akom, E., Kumadoh, J., and Opoku, J. 2016. Bryophytes of Atewa Forest, Eastern Region, Ghana. *J. Bryol.* 38: 211-222.
- Holz, I. and Gradstein, S. R. 2005. Phylogeography of the bryophyte floras of oak forests and páramo of the Cordillera de Talamanca, Costa Rica. *J. Biogeogr.* 32: 1591-1609.
- Holz, I., Gradstein, S. R., Heinrichs, J., and Kappelle, M. 2002. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane Quercus forest. *Bryologist* 105: 334-348.
- Hylander, K., Pócs, T., and Nemomissa, S. 2010. Liverworts of southwest Ethiopian montane forests: Ecological and biogeographical notes. *J. Bryol.* 32: 92-100.
- Hylander, K., Nemomissa, S., and Hedenäs, L. 2017. Mosses of southwest Ethiopian montane forests – notes on their occurrence pattern and many new country records. *J. Bryol.* 39: 342-352.
- Inoue, H. 1989. The bryophytes of Sabah (North Borneo) with special reference to the BRYOTROP transect of Mount Kinabalu. V. *Plagiochila* (Plagiochilaceae, Hepaticae). *Willdenowia* 18: 555-567.
- Ireland, R. R. 1992. The moss genus *Isopterygium* (Hypnaceae) in Latin America. *Trop. Bryol.* 6: 111-132.
- Jones, E. W., Wigginton, M. J., Kerckhove, O. Van de, and Duckett, J. G. (eds.). 2004. E. W. Jones's Liverwort and Hornwort Flora of West Africa. National Botanic Garden (Belgium), Meise, 443 pp.
- Jordan, C., Golley, F., Hall, J. D., and Hall, J. 1980. Nutrient scavenging of rainfall by the canopy of an Amazonian rain forest. *Biotropica* 12: 61-66.
- Karlin, E. F., Hotchkiss, S. C., Boles, S. B., Stenøien, H. K., Hassel, K., Flatberg, K. I., and Shaw, A. J. 2012. High genetic diversity in a remote island population system: Sans sex. *New Phytol.* 193: 1088-1097.
- Kautz, T. and Gradstein, S. R. 2001. On the ecology and conservation of *Spruceanthus theobromae* (Lejeuneaceae, Hepaticae) from Western Ecuador. *Bryologist* 104: 607-612.
- Kürschner, H. 2003a. Epiphytic bryophyte communities of southwestern Arabia – phytosociology, ecology and life strategies. *Nova Hedw.* 77: 55-71.
- Kürschner, H. 2003b. The *Ricciatum jovet-astii-argenteolimbatum* ass. nov. of the Jabal Arays area, Yemen-life strategies of a remarkable xerotropical African bryophyte community. *Nova Hedw.* 76: 399-413.
- Kürschner, H. and Frey, W. 2011. Liverworts, mosses and hornworts of southwest Asia (Marchantiophyta, Bryophyta, Anthocerotophyta). *J. Cramer, Stuttgart*, 240 pp.
- Kürschner, H. and Onraedt, M. 1990. Quelques bryophytes de la République de Djibouti (Territoire français de Afars et des Issas). [Some bryophytes of the Republic of Djibouti (French Territory of Afars and Issas).]. *Nova Hedw.* 50: 181-190.
- Kürschner, H. and Parolly, G. 1999. Pantropical epiphytic rain forest bryophyte communities – Coeno-syntaxonomy and floristichistorical implications. *Phytocoenologia* 29: 1-52.
- Lee, G. E., Pócs, T., Gradstein, S. R., Damanhuri, A., and Latiff, A. 2018. Abundant but neglected: Past and present of liverwort (Marchantiophyta) studies in Malaysia. *Cryptog. Bryol.* 39: 83-91.
- Mägdefrau, K. 1983. The bryophyte vegetation of the forests and páramos of Venezuela and Colombia. *Nova Hedw.* 38: 1-63.
- Marline, L., Andriamiarisoa, R. L., Bardat, J., Chuah-Petiot, M., Hedderson, T. A., Reeb, C., Strasberg, D., Wilding, N., and Ah-Peng, C. 2012. Checklist of the bryophytes of Madagascar. *Cryptog. Bryol.* 33: 199-255.
- McClure, H. 1966. Flowering, fruiting and animals in the canopy of a tropical rainforest. *Malaysian Forester* 29: 182-203.
- Menzel, M. 1992. Preliminary checklist of the mosses of Peru. *J. Hattori Bot. Lab.* 71: 175-254.
- Merckx, V. S., Hendriks, K. P., Beentjes, K. K., Mennes, C. B., Becking, L. E., Peijnenburg, K. T., Afendy, A., Arumugam, N., Boer, H. de, Biun, A., Buang, M. M., Chen, P.-P., Bhung, A. Y. C., Dow, R., Feijen, F. A. A., Jeijen, H., Jeijen-van Soest, C., Geml, J., Geurts, R., Gravendeel, B., Hovenkamp, P., Imbun, P., Ipor, I., Janssens, S. B., Mocqué, M., Kappes, H., Khoo, E., Koomen, P., Lens, F., Majapun, R. J., Morgado, L. N., Neupane, S., Nieser, N., Pereira, J. T., Rahman, H., Sabran, S., Sawng, A., Schwallier, R. M., Shim, P.-S., Smit, H., Sol, N., Spait, M., Stech, M., Stokvis, F., Sugau, J. B., Suleiman, M., Sumail, S., Thomas, D. C., Tol, J. van, Tuh, F. Y. Y., Yahya, B. E., Nais, J., Repin, R., Lakim, M., and Schilthuizen, M. 2015. Evolution of endemism on a young tropical mountain. *Nature* 524: 347-350.
- Miehe, G. and Miehe, S. 1994. East African bryophytes. XII. Bryophytes from Bale Mountains, SE Ethiopia. 1. Phytoecological introduction. *Fragm. Flor. Geobot.* 39: 165-219.
- Mohamed, M., A. H. and Tan, B. C. 1988. A checklist of mosses of Peninsular Malaysia and Singapore. *Bryologist* 91: 24-44.
- Montfoort, D. and Ek, R. 1990. Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guyana. *Institute of Systematic Botany, Utrecht*.
- Moreno, E. J. 1992a. Revisión histórica de la briología en Venezuela. *Trop. Bryol.* 6: 139-146.
- Moreno, E. J. 1992b. Aproximación al conocimiento de las briofitas de Venezuela. *Trop. Bryol.* 6: 147-156.
- Motito, A., Potrony, M. E., and Reyes, M. D. 1992. Estado actual y perspectivas futuras del estudio de los musgos cubanos. [Current status and future perspectives of the study of Cuban mosses.]. *Trop. Bryol.* 6: 157-160.
- Müller, F. and Flügge, H.-J. 2016. New records of bryophytes from the biosphere reserve Kafa in Ethiopia. *Herzogia* 29: 190-195.

- Nees von Esenbeck, C. G. 1830. *Enumeratio plantarum cryptogamicarum Javae et insularum adiacentium*. Grass, Barth & Co., Breslau, 86 pp.
- Ninh, T. 1993. Mosses of the Tam Dao Mountains, Vietnam. *Bryologist* 96: 573-581.
- Norhazrina, N., Wang, J., Hagborg, A., Geffert, J. L., Mutke, J., Gradstein, S. R., Baselga, A., Vanderpoorten, A., and Patiño, J. 2016. Tropical bryophyte floras: A homogeneous assemblage of highly mobile species? Insights from their spatial patterns of beta diversity. *Bot. J. Linn. Soc.* 183: 16-24.
- Odu, E. A. 1981. Reproductive phenology of some tropical African mosses. *Cryptog. Bryol. Lichénol.* 2: 91-99.
- Odu, E. A. 1982. Phenology of west tropical African mosses. *J. Hattori Bot. Lab.* 52: 283-285.
- Oliveira, H. C. and Alves, M. H. 2007. Adições à brioflora do Estado do Ceará, Brasil. [Additions to the bryoflora of the State of Ceará, Brazil.]. *Rodriguésia* 58: 1-11.
- Oliveira, H. C. and Bastos, C. J. P. 2009. *Antóceros* (Anthocerotophyta) e hepáticas talosas (Marchantiophyta) da Chapada da Ibiapaba, Ceará, Brasil. [*Anthoceros* (Anthocerotophyta) and thallose hepatics (Marchantiophyta) from the Chapada da Ibiapaba, Ceará, Brazil.]. *Rodriguésia* 60: 1-8.
- O'Shea, B. 1995. Checklist of the mosses of sub-Saharan Africa. *Bryo. Divers. Evol.* 10: 91-198.
- O'Shea, B. J. 1997a. The mosses of sub-Saharan Africa 1. A review of taxonomic progress. *J. Bryol.* 19: 509-513.
- O'Shea, B. J. 1997b. The mosses of sub-Saharan Africa 2. Endemism and biodiversity. *Trop. Bryol.* 13: 75-86.
- O'Shea, B. 2002. Sematophyllaceae: A tropical moss family with species in Britain. *Bull. Brit. Bryol. Soc.* 78: 25-27.
- O'Shea, B. J. 2003. Bryogeographical relationships of the mosses of Sri Lanka. *J. Hattori Bot. Lab.* 93: 293-304.
- Oyesiku, O. O. 2012. A review of Nigerian bryophytes: Past, present and future. *Afr. J. Agric Res* 7: 4352-4356.
- Parker, G., Smith, A., and Hogan, K. 1992. Access to the upper forest canopy with a large tower crane. *BioScience* 42: 664-670.
- Patiño, J., Carine, M., Fernández-Palacios, J. M., Otto, R., Schaefer, H., and Vanderpoorten, A. 2014. The anagenetic world of spore-producing land plants. *New Phytol.* 201: 305-311.
- Perry, D. 1978. A method of access into the crowns of emergent trees. *Biotropica* 10: 155-157.
- Petit, E. 1992. Keys for the determination of families of pleurocarpous mosses of Africa. Extracted from: Clés pour la détermination des familles et des genres des mousses pleurocarpes (Muscis) d'Afrique. *Bull. Jard. Bot. Nat. Belg.* 48: 135-181 (1978). Translated by M. J. Wigginton and C. R. Stevenson, with some nomenclatural updating. Published online at http://www.nhm.ac.uk/hosted_sites/bbstbg/pleuro_key.pdf. Accessed 19 September 2018.
- Petit, E. and Symons, F. 1974. Les bryophytes des bois artificiels de *Cupresses* et d'*Acacia* au Burundi. Analyse factorielle de la végétation bryophytique. *Bull. Jard. Bot. Nat. Belgique* 44: 219-247.
- Piippo, S. 1994a. Phytogeography and habitat ecology of Western Melanesian endemic Hepaticae. *J. Hattori Bot. Lab.* 75: 275-293.
- Piippo, S. 1994b. On the bryogeography of Western Melanesian Lejeuneaceae, with comments on their epiphyllous occurrence. *Trop. Bryol.* 9: 43-58.
- Piippo, S., Koppen, T., and Norris, D. H. 1987. Endemism of the bryophyte flora in New Guinea. *Symp. Biol. Hung* 35: 361-372.
- Pisa, S., Werner, O., Vanderpoorten, A., Magdy, M., and Ros, R. M. 2013. Elevational patterns of genetic variation in the cosmopolitan moss *Bryum argenteum* (Bryaceae). *Amer. J. Bot.* 100: 2000-2008.
- Pócs, T. 1969. A short survey of the *Bazzania* of North Vietnam. *J. Hattori Bot. Lab* 32: 79-94.
- Pócs, T. 1975. Affinities between the bryoflora of East Africa and Madagascar. *Boissiera* 24: 125-128.
- Pócs, T. 1976. Correlations between the tropical African and Asian bryofloras, I. *J. Hattori Bot. Lab.* 41: 95-106.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 59-104.
- Pócs, T. 1987. Changes in the biomass and productivity of bryophytes in East African rainforests. XIV Internat. Bot. Congress Abstracts, p. 264.
- Pócs, T. 1990. The exploration of East Africa bryoflora. *Trop. Bryol.* 2: 177-191.
- Pócs, T. 1992. Correlation between the tropical African and Asian bryofloras. II. *Bryobrothera* 1: 35-47.
- Pócs, T. 1998. Bryophyte diversity along the Eastern Arc. *J. E. Afr. Nat. Hist.* 87: 75-84.
- Pócs, T. 2011. East African bryophytes XXIX. The *Ceratolejeunea* (Lejeuneaceae) species of the Indian ocean islands. *Polish Bot. J.* 56: 131-153.
- Pócs, T. and Chantanaorrapint, S. 2016. Southern Thailand Bryophytes III: A preliminary study on non-epiphyllous taxa in lowland areas. *Songklanakarin J. Sci. Technol.* 38: 311-318.
- Pursell, R. A. 1973. Un censo de los musgos de Venezuela. *Bryologist* 76: 473-500.
- Ramsay, H. P. and Cairns, A. 2004. Habitat, distribution and the phytogeographical affinities of mosses in the Wet Tropics bioregion, north-east Queensland, Australia. *Cunninghamia* 8: 371-408.
- Ramsay, H. P., Streimann, H., and Harden, G. 1987. Observations on the bryoflora of Australian rain forests. *Symp. Biol. Hung.* 35: 605-620.
- Raxworthy, C. J., Pearson, R. G., Rabibisoa, N., Rakotondrazafy, A. M., Ramanamanjato, J. B., Raselimanana, A. P., Wu, S., Nussbaum, R. A., and Stone, D. A. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: A preliminary appraisal for the highest massif in Madagascar. *Global Change Biol.* 14: 1703-1720.
- Redfearn, P. L. 1990. Tropical component of the moss flora of China. *Trop. Bryol.* 2: 201-222.
- Reenen, G. B. A. van and Gradstein, S. R. 1983. Studies on Colombian cryptogams. XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Bot. Neerl.* 32: 163-175.
- Reenen, G. B. A. van and Gradstein, S. R. 1984. Analisis de la vegetación de briofitas en el transecto Buritca – La Cumbre (Sierra Nevada de Santa Marta, Colombia). [Analysis of the bryophyte vegetation in the Buritca – La Cumbre transect (Sierra Nevada de Santa Marta, Colombia).]. *Studies on Tropical Andean Ecosystems* 2: 189-202.
- Reese, W. R. 1993. Calymperaceae. *Flora Neotropica Monograph* 58: 1-101. New York Botanical Garden, USA.

- Reinwardt, C. G. C., Blume, C. L., and Nees von Esenbeck, C. G. 1824. *Hepaticae Javanicae, editae coniunctis studiis et opera. Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum* 12: 181-238.
- Richards, P. W. 1954. Notes on the bryophyte communities of lowland tropical rain forest, with special reference to Moraballi Creek, British Guiana. *Vegetatio* 6: 319-328.
- Richards, P. W. 1991. A bryologist in British Guiana and the West Indies. *J. Bryol.* 16: 437-441.
- Ros, R. M., Cano, M. J., and Guerra, J. 1999. Bryophyte checklist of northern Africa. *J. Bryol.* 21: 207-244.
- Rowe, K. C., Achmadi, A. S., and Esselstyn, J. A. 2016. A new genus and species of omnivorous rodent (Muridae: Murinae) from Sulawesi, nested within a clade of endemic carnivores. *J. Mammal.* 97: 978-991.
- Rubasinghe, S. C., and Long, D. G. 2014. Bryophytes of Sri Lanka: A review of past exploration and taxonomic research and priorities for the future. *J. Bryol.* 36: 259-270.
- Salazar Allen, N., Gradstein, S. R., and Churchill, S. P. 1996. Bryophytes as non-woody biodiversity indicators: A guide to the bryophytes of tropical America. A report. *An. Inst. Biol. Univ. Nac. Auton. Mexico* 67: 59-65.
- Sande Lacoste, C. M. van der. 1857 ("1856"). *Synopsis Hepaticarum Javae. Verhand. Koninklijke Akad. Wetenschappen* 5: 1-112.
- Sande Lacoste, C. M. van der. 1864. *Hepaticae. Jungermanniae Archipelagi Indig. adiectis quibusdam speciebus Japonicis. Ann. Musei Bot. Lugduno-Batavi* 1: 287-314.
- Sastre-de Jesus, I. and Santiago-Valentín, E. 1996. Bryology in Puerto Rico. Knowledge prior to and after the scientific survey of Porto Rico and the Virgin Islands. *Ann. N. Y. Acad. Sci.* 115: 111-122.
- Schäfer-Verwimp, A., Lehnert, M., and Nebel, M. 2013. Contribution to the knowledge of the bryophyte flora of Ecuador. *Phytotaxa* 128: 1-63.
- Schiffner, V. 1900. *Die Hepaticae der Flora von Buitenzorg, Erster Band. Brill, Leiden.*
- Schofield, W. B. and Crum, H. A. 1972. Disjunctions in bryophytes. *Ann. Missouri Bot. Gard.* 59: 174-202.
- Schuster, R. M. 1982. Generic and familial endemism in the hepatic flora of Gondwanaland: Origins and causes. *J. Hattori Bot. Lab.* 52: 3-35.
- Schuster, R. M. 1988. Ecology, reproductive biology and dispersal of the Hepaticae in the Tropics. *J. Hattori Bot. Lab.* 64: 237-269.
- Scott, G. A. M. 1985. *Southern Australian Liverworts. Australian Flora and Fauna Series Number 2, Australian Government Publishing Service, Canberra, 216 pp.*
- Seaward, M. R. D., Ellis, L. T., Pócs, T., and Wigginton, M. J. 2006. Bryophyte flora of the Chagos Archipelago. *J. Bryol.* 28: 11-19.
- Sharp, A. J., Crum, H. A., and Eckel, P. M. (eds.). 1994. *The Moss Flora of Mexico. 2 vols. New York Botanical Garden, N. Y.*
- Shaw, A. J., Cox, C., and Goffinet, B. 2005. Global patterns of moss diversity: Taxonomic and molecular inferences. *Taxon* 54: 337-352.
- Silva, M. P. P., Kamino, L. H., and Pôrto, K. C. 2014. Is the current network system of protected areas in the Atlantic Forest effective in conserving key species of bryophytes? *Trop. Conserv. Sci.* 7: 61-85.
- Sjögren, E. 1997. Epiphyllous bryophytes in the Azores Islands. *ARQUIPÉLAGO. Ciências Biol. Marinhas. [Life Marine Sci.]* 15: 1-49.
- Spruce, R. 1884-1885. *Hepaticae Amazonicae et Andinae. Trans. Proc. Bot. Soc. Edinburgh* 15: 1-588. [published in two parts, the first in 1884 as 15(1): 1-308, the second in 1885 as 15(2): 309-588].
- Stark, R. M. 1860. *Popular History of British Mosses. Edn. 1. George Routledge & Sons, London, 348 pp.*
- Steere, W. C. 1948. Contribution to the bryogeography of Ecuador I. A review of the species of Musci previously reported. *Bryologist* 51: 65-167.
- Stevenson, L. A., González-Orozco, C. E., Knerr, N., Cargill, D. C., and Miller, J. T. 2012. Species richness and endemism of Australian bryophytes. *J. Bryol.* 34: 101-107.
- Sukharak, P. and Chantanaorrapint, S. 2014. Bryophyte studies in Thailand: Past, present, and future. *Cryptog. Bryol.* 35: 5-17.
- Suleiman, M., Akiyama, H., and Tan, B. C. 2006. A revised catalogue of mosses reported from Borneo. *J. Hattori Bot. Lab.* 99: 107-183.
- Tan, B. C. and Iwatsuki, Z. 1999. Four hot spots of moss diversity in Malesia. *Bryobrothera* 5: 247-252.
- Tan, B., Ho, B.-C., and Lim, Y.-H. Singapore Science Centre. 2008. *A Guide to the Mosses of Singapore. Science Centre Singapore.*
- Timme, S. L. 1985. Bryophyte floristic and ecological studies of the Amazon River basin, Department of Loreto, Peru. Ph.D. dissertation, Mississippi State University, 280 pp.
- Tixier, P. 1980. Contribution to the bryological knowledge of Malaysia III. Cameron Highlands, mosses and epiphyllous liverworts. *Nova Hedw.* 32: 377-392.
- Uribe-M., J. and Gradstein, S. R. 2003. Type studies on *Frullania* subgenus *Meteoriopsis* (Hepaticae). I. The lectotypification of the genus. *Cryptog. Bryol.* 24: 193-207.
- Valente, E. B., Pôrto, K. C., and Bastos, C. J. P. 2013. Species richness and distribution of bryophytes within different phytogeographies in the Chapada Diamantina region of Brazil. *Acta Bot. Brasil.* 27: 294-310.
- Villalreal, J. C., Hässel de Menéndez, G., and Salazar Allen, N. 2007. *Nothoceros superbus* (Dendrocerotaceae), a new hornwort from Costa Rica. *Bryologist* 110: 279-285.
- Visnadi, S. R. 2015. *Brioflora do Parque Estadual Intervales, São Paulo, Brasil: Uma importante área para conservação da biodiversidade da Mata Atlântica do sudeste brasileiro. [Brioflora of the Intervales State Park, São Paulo, Brazil: An important area for the conservation of the biodiversity of the Atlantic Forest of southeastern Brazil.]. Bol. Mus Paraense Emílio Goeldi, Ciên. Nat.* 10: 105-125.
- Vital, D. M. and Visnadi, S. R. 1994. Bryophytes of Rio Branco Municipality, Acre, Brazil. *Trop. Bryol.* 9: 69-74.
- Wang, J., Vanderpoorten, A., Hagborg, A., Goffinet, B., Laenen, B., and Patiño, J. 2016. Evidence for a latitudinal diversity gradient in liverworts and hornworts. *J. Biogeogr.* 44: 487-488.
- Whitacre, D. 1981. Additional techniques and safety hints for climbing tall trees, and some equipment and information sources. *Biotropica* 13: 286-291.
- Whitmore, T. C. 1998. *An Introduction to Tropical Rain Forest. 2nd edn. Oxford University Press, 282 pp.*
- Wigginton, M. J. 2001a. British Bryological Society expedition to Mulanje Mountain, Malawi. 15. Lejeuneaceae, and the occurrence and frequency of foliicolous taxa. *Trop. Bryol.* 20: 83-96.
- Wigginton, M. J. 2001b. A small collection of bryophytes from Ethiopia. *Trop. Bryol.* 20: 27-29.

- Wolf, J. H. D. 1993a. Epiphyte communities of tropical montane rain forest in the northern Andes. I. Lower montane communities. *Phytocoenologia* 22: 1-52.
- Wolf, J. H. D. 1993b. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Missouri Bot. Gard.* 80: 928-960.
- Wołowski, K., Godzik, B., and Wójcicki, J. J. (eds.). 2014. Festschrift for Tamás Pócs on the occasion of his 80th. birthday. Parts 1 and 2. *Polish Bot. J.* 58, parts 1, 2.
- Yano, O. 1981. A checklist of Brazilian mosses. *J. Hattori Bot. Lab.* 50: 279-456.
- Yano, O. 2011. Catálogo de musgos Brasileiros: Literatura original, basíônimo, localidade-tipo e distribuição geográfica. [Catalog of Brazilian mosses: Original literature, basíônimo, locality-type and geographical distribution.]. São Paulo, Instituto de Botânica.
- Zotz, G. and Vollrath, B. 2003. The epiphyte vegetation of the palm *Socratea exorrhiza* – Correlations with tree size, tree age and bryophyte cover. *J. Trop. Ecol.* 19: 81-90.

CHAPTER 8-3

TROPICS: EPIPHYTE ECOLOGY, PART 1

TABLE OF CONTENTS

Water Relations.....	8-3-4
Water Content.....	8-3-4
Growth Forms and Life Forms.....	8-3-5
Osmotic Potential.....	8-3-10
Desiccation Recovery	8-3-12
Rainfall Interception	8-3-12
Fog Interception	8-3-14
Microclimate	8-3-15
Nutrient Dynamics	8-3-18
Rainfall vs Throughfall.....	8-3-19
Nitrogen Dynamics	8-3-20
Pulse Release	8-3-21
Keystone Resource.....	8-3-22
Canopy Roots.....	8-3-23
Productivity and Biomass.....	8-3-12
Epiphyte Litterfall	8-3-31
Summary	8-3-32
Acknowledgments.....	8-3-33
Literature Cited	8-3-33

CHAPTER 8-3

TROPICS: EPIPHYTE ECOLOGY, PART 1



Figure 1. Celaque cloud forest in tropical Honduras. Photo by Josiah Townsend, with permission.

Barkman (1958) has contributed the definitive work on cryptogamic epiphytes (bryophytes, lichens) in 628 pages. It provides an account of the ecology and adaptations as they were known at the time and is the "bible" on cryptogamic epiphyte ecology. The work is restricted to temperate regions and does not treat tropical epiphytic bryophytes, which were very little known at the time. Nevertheless, much of the ecological information provided in this book is also valid for the tropics.

I was surprised to learn that approximately 10% of the tracheophytes are epiphytes (Prosperi & Michaloud 2001). It was not a surprise to learn that these are almost exclusively tropical, where they represent up to 25% of the tracheophytes. Overall, bryophytes comprised 40% of the epiphytic biomass in a neotropical cloud forest in Costa Rica (Nadkarni 1984) compared to 6% in the leeward cloud forest (Ingram & Nadkarni 1993). In both forests, bryophytes were most abundant among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dryer 1980).

The epiphytic habitat (Figure 1) is the most diverse one for tropical rainforest bryophytes, with 14 of the 15 main bryophyte families being predominantly epiphytic (Figure 1) (Gradstein & Pócs 1989). This is where the greatest bryophytic biomass of the rainforests occurs (Hofstede *et al.* 1993). Not surprisingly, the dry weight of epiphytes in the tropics is generally less than that shown in a New Zealand study (Hofstede *et al.* 2001), where lower temperatures and shorter dry periods are more favorable for bryophytes. In a New Zealand lowland, a single tree supported 61 tracheophyte species compared to 94 non-tracheophytes (lichens included). Pócs (1980) found a positive correlation between the amount of "surplus" rainfall (rainfall above 100 mm/month) and the epiphytic biomass in rainforest climates.

Among the early studies on bryophytic epiphytes, one must note the Japanese studies (Horikawa 1932, 1939, 1948, 1950; Kamimura 1939; Horikawa & Nakanishi 1954; Hattori & Noguchi 1954; Hattori & Kanno 1956; Hattori *et al.* 1956; Hattori 1966; Hattori & Iwatsuki 1970; Iwatsuki 1960, 1961, 1962, 1963a, b; Iwatsuki & Hattori 1955, 1956a, b, c, d, e, f, 1957, 1959a, b, 1965a, 1965b, 1966,

1968, 1970, 1987; Mizutani 1966). Hosokawa (1950, 1951, 1953, 1954) and coworkers (Hosokawa & Kubota 1957; Hosokawa & Odani 1957; Hosokawa & Omura 1959; Hosokawa *et al.* 1954, 1957, 1964) pioneered in describing epiphytic communities. Another important early study from Asia is the work by Tixier (1966) on epiphytic communities in Vietnam. Went (1940) discussed the sociology of tracheophytic epiphytes of Java.

Gradstein *et al.* (2007) compared the species richness on various substrates in southern Ecuador. This study demonstrated the preponderance of epiphytes there (Figure 2).

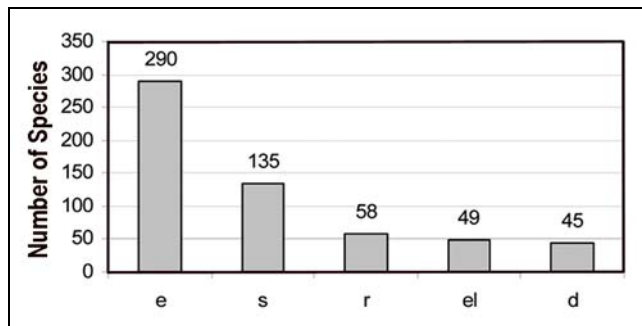


Figure 2. Substrate types of liverworts and hornworts at Reserva Biológica San Francisco, southern Ecuador. Number above each bar is number of species on that substrate type; e = epiphytic (bark); s = soil (incl. humus); r = rock; el = epiphyllous (living leaves); d = decaying wood. From Gradstein *et al.* 2007.

Frahm (1990a, 1994) found that in Borneo lowland and montane rainforests, even bark texture (smooth, fissured, flaky, or striped) made a difference in the epiphytic communities that developed. All bryophytes were considered to be acidophilic, with epiphytic bryophytes having no significant correlation with pH. On the other hand, rich concentrations of Na, K, and Mg seemed to be important in the substrate.

Akiyama *et al.* (2001) contributed to the knowledge of the Borneo bryophyte flora through two expeditions to the Kinabalu National Park in Malaysia. They reported 203 moss species and 31 liverwort species, with 25 species added to the checklist for the park and 17 new to Borneo.

Kürschner and Parolly (1998a) examined **pantropical** (covers tropical regions of both eastern & western hemispheres) features that determined distribution of the epiphytic bryophytes. They found that distribution is correlated with structural parameters of the tree stands and with temperature zone intervals. Using only **supraspecific** taxa (*i.e.*, above the species level) they concluded that communities at low altitudes and those at high altitudes, respectively, resemble each other more pantropically than do lowland and montane communities on the same continent. Kürschner and coworkers were instrumental in elucidating epiphytic bryophyte communities in Africa (Kürschner 1995a, b).

Kürschner and Parolly (1999) sought to derive a consistent system for classifying the tropical epiphytes on a pantropical basis. Instead of using species, they used higher classification levels. For the lowland and submontane tropics they recognized the **Coeno-Ptychanthetalia** (Figure 3), whereas in the montane zones they recognized the **Coeno-Bazzanio-Herbertetalia**

(Figure 4-Figure 5). Using this thinking, they found that the low-altitudinal and high-altitudinal communities are more similar to each other pantropically than the communities of lowland and montane vegetation units occurring on the same continent.



Figure 3. *Ptychanthus striatus*; the *Ptychanthalia* synusia is typical in the lowland and submontane tropics, with pantropic distribution. Photo by Li Zhang, with permission.



Figure 4. *Bazzania* sp. from the Neotropics, a genus characteristic of the **Coeno-Bazzanio-Herbertetalia** in the montane zone. Photo by Michael Luth, with permission.



Figure 5. *Herbertus aduncus*, in a genus characteristic of the **Coeno-Bazzanio-Herbertetalia** in the montane zone. Photo by Barry Stewart, with permission.

Much remains to be found among the tropical bryophytes. Lee and Pócs (2018) have recently added to our knowledge of the distribution of the large genus *Lejeunea* (Figure 6), describing the new species *Lejeunea konratii* from Fiji.



Figure 6. *Lejeunea flava*; *L. konratii* was a new species in Java in 2018. Photo by Jia-dong Yang, through Creative Commons.

Some epiphytic bryophytes are **facultative**, growing on other types of substrate. Ando (1969) reported that the epiphytic bryophytes on *Buxus microphylla* var. *insularis* (= *B. sinica* var. *insularis*; Figure 7) also grew on limestone ridges in Taishaku.



Figure 7. *Buxus microphylla*. Epiphytic mosses of this species also grow on limestone ridges. Photo by Sage Ross, through Creative Commons.

Frahm and Kürschner (1989) investigated factors related to bryophyte success on trees. Rhoades (1995) provided an extensive review on the nontracheophyte epiphytes of the canopy, including distribution, abundance, and ecological roles, but this paper mainly focuses on temperate forests.

Water Relations

The distribution of epiphytic bryophytes in the tropics seems to be all about water. The bryophytes in the crowns of the trees generally are more desiccation-resistant than are those at the tree base (Hosokawa & Kubota 1957; Hosokawa *et al.* 1964).

Water is always a primary limiting factor for epiphytes, and in the tropics the daily change from wet to dry can be particularly problematic (Johnson & Kokila 1970). For some species in the saturated rainforests, as little as 4 hours of exposure to a relative humidity of 63% or less can result in damage. Thus, such sensitive species often live on the wettest sides of the trees. Within a range of 10-76% humidity for four hours, two groups of mosses emerged. One group had low resistance, but the other had a high resistance to desiccation. This latter group of species grew in microhabitats of the forest with low humidity.

Löbs *et al.* (2019) opined that our understanding of the role of the extensive epiphytic bryophyte cover was largely unknown, noting their potential importance in biosphere-atmosphere exchange, climate processes, and nutrient cycling. Their water content could have important impact on local, regional, and even global biogeochemical processes. The researchers measured a vertical gradient from the Amazon Tall Tower Observatory in the Amazonian rainforest and determined that only minor variations occurred in the monthly average ambient light intensity above the canopy, but that different patterns emerged at different heights. At 1.5 m, the values were extremely low, exceeding 5 $\mu\text{mol m}^{-2}$ photosynthetic photon flux density only 8% of the time. These values differed little throughout the year. The temperatures likewise showed only minor variation throughout the year, with larger values and more height dependence during the dry season. Water levels, on the other hand showed more variability. At higher levels they were affected by the frequency of wetting and drying; at low levels near the forest floor they retained water over a longer time period. They concluded that water content is the deciding factor for overall physiological activity, with light intensity determining whether net photosynthesis or dark respiration occurs. Temperature was of only minor importance. Light was limiting on the forest floor; in the canopy the bryophytes had to withstand a larger variation in microclimatic conditions.

Water Content

Klinge (1963) reported on the epiphyte humus from El Salvador. Their role in forest water and nutrient dynamics, however, seemed to attract little attention. Water content of bryophytic epiphytes in an old-growth forest in Costa Rican cloud forest reached maximum values of 418% of dry weight, with a minimum of 36% (Köhler *et al.* 2007). The epiphytic bryophytes experienced more dynamic wetting and drying cycles than did the canopy humus. The maximum water loss from bryophytes through evaporation was 251% (dry weight), whereas it was only 117% from the canopy humus, following three days of sunny weather with no intervening precipitation.

Pócs (1989) estimated that high altitude epiphytic bryophytes in Tanzania can absorb up to 30,000 L ha⁻¹ of water during one rainstorm. When high humidity and high

temperatures occur at the same time, as they often do, they cause respiratory losses that cannot be balanced by photosynthesis in these C_3 plants, thus limiting their productivity, especially in the lowland forests (Richards 1984, Frahm 1990b).

Karger *et al.* (2012) measured the relationship of bryophyte cover to air humidity at two elevation ranges in the tropics. When the highland site (1800-3500 m asl) was considered separately from the lowland site (<1800 m asl) there was a significant relationship between bryophyte cover and relative air humidity. Temperature related to cover in the lowlands only. They confirmed that bryophyte cover is a good proxy for relative air humidity along the elevational gradient in the tropics, proposed earlier by van Reenen and Gradstein (1983).

Müller and Frahm (1998) compared the water-holding capacity of epiphytes in a montane rainforest in the Andes of Ecuador. They found an average of 0.57 L m⁻² on the trunks, 19.51 L m⁻² on branches, and 4.16 L m⁻² on twigs. This is ten times the dry weight on branches, but only three times on twigs. Using a representative tree of 27 m height, which has an average of 65.4 kg dry weight of epiphytes, they calculated that the epiphytic bryophytes on one such tree could store 669 liters of water.

Growth Forms and Life Forms

Several life forms and their role in water relations have already been discussed in an earlier chapter. For definitions, illustrations, and examples, see Chapter 4-5 in the Physiology volume.

Kürschner (1990) looked at the distribution of life forms and water-bearing and water-storing structures in epiphytic moss communities on Mt. Kinabalu, North Borneo. Norris (1990) concluded that water relations must be understood along at least four dimensions: hydration/dehydration frequency; duration of hydration; duration of dehydration; degree of water loss. More recent studies of xerophytic bryophytes suggest that the rate of drying is also important (Greenwood & Stark 2014). Norris further concluded that **large colonies** generally maintain hydration longer than do smaller colonies. Water can be conducted laterally among contiguous clones. Separated **tufts** and **cushions**, on the other hand, may store more water, but they contribute little to transfer of water over the surface of the host tree. In the tropical rainforests, the mass of the bryophytic epiphytes is typically larger than that found in temperate forests. The biomass is reduced as a result of disturbance, probably due to increased opportunity for desiccation with increased isolation and wind movement. This further results in the loss of water transfer and reduction in both water and mineral retention. Norris cited the *Braunfelsia* (moss; Figure 8) community in Papua New Guinea as an example of sensitivity to deforestation and resulting increase in dehydration frequency of adult plants.

Working in the tropical montane oak-bamboo forest of Costa Rica, Romero *et al.* (2006) conducted investigations on four **pendent** bryophyte species, listed from most protected to most exposed: *Phyllogonium viscosum* (Figure 9), *Pilotrichella flexilis* (Figure 10), *Dendropogonella rufescens* (Figure 11), and *Frullania convoluta* (Figure 12). They found that the most exposed species had higher light saturation and compensation

points, higher dark respiration rates, more chlorophyll, higher chlorophyll *a:b* ratios, and higher N concentrations. Contrary to expectations, the most exposed species had the lowest water content at full saturation. Rate of water loss differed little among the species. The rather exposed moss *Dendropogonella rufescens* had a substantially higher moisture compensation point for carbon uptake than did the other three species. The researchers concluded that density, size, and arrangement of leaves, as well as clump architecture, defined the physiological patterns of water storage and transport they observed.



Figure 8. *Braunfelsia dicranoides*. The *Braunfelsia* community is especially sensitive to deforestation in Papua New Guinea. Photo from the Natural History Museum, London, through Creative Commons.



Figure 9. *Phyllogonium viscosum*, a **pendent** species requiring the most protected part of the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 10. *Pilotrichella flexilis nudiramulosa*, a **pendent** species requiring a protected part of the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Claudio Delgadillo Moya, with permission.



Figure 11. *Dendropogonella* sp.; *D. rufescens* has a substantially higher moisture compensation point for carbon uptake than the other three tropical species tested. Photo by Claudio Delgadillo Moya, with permission.

Kürschner and Parolly (1998b) discussed adaptations to water conduction and storing. The **mat** life form that is typical of lowland habitats correlates with such water-holding structures as leaf lobules (Figure 13) [especially **Lejeuneaceae** (Figure 6)] and water sacs as well as rhizoids that can act like sponges to hold and move water in capillary spaces. In addition to these, Frey *et al.* (1990) included **alar cells** (Figure 14), **vittae** (row of elongated cells down center of leaf, only one cell deep; Figure 15), and **ocelli** (darkened cells in row in leafy liverwort leaf; Figure 13, Figure 16) as characteristic of epiphytic

bryophytes in the lowland forest of Mt. Kinabalu, North Borneo. Rhizoid discs (Figure 17) maintain attachment. In areas with high humidity in the montane belt, the **mat** form is replaced by **fan** (Figure 21), **weft**, and **pendant** (Figure 9-Figure 12, Figure 34-Figure 35) life forms that are able to obtain water from fog and mist (**fog-stripping**). Fine leaves (Figure 10) or deeply divided leaves are able to capture this water.



Figure 12. *Frullania convoluta*, a **pendent** species requiring the least protection by the tree in the tropical montane oak-bamboo forest of Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 13. *Frullania tamarisci* with **ocelli** (dark lines of leaf cells) and leaf **lobules**. Photo by Hermann Schachner, through Creative Commons.

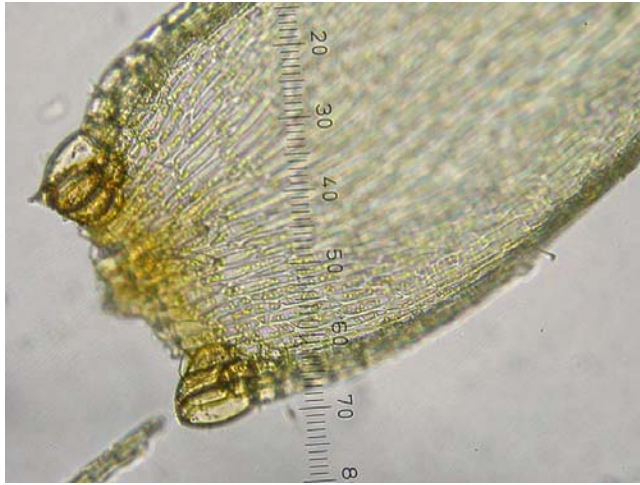


Figure 14. *Pylaisiadelphina tenuirostris* with inflated alar cells. Photo by Bob Klips, with permission.



Figure 15. *Herbertus aduncus* leaf vittae (note longer cells running down midleaf. Photo from Botany Website, UBC, with permission.

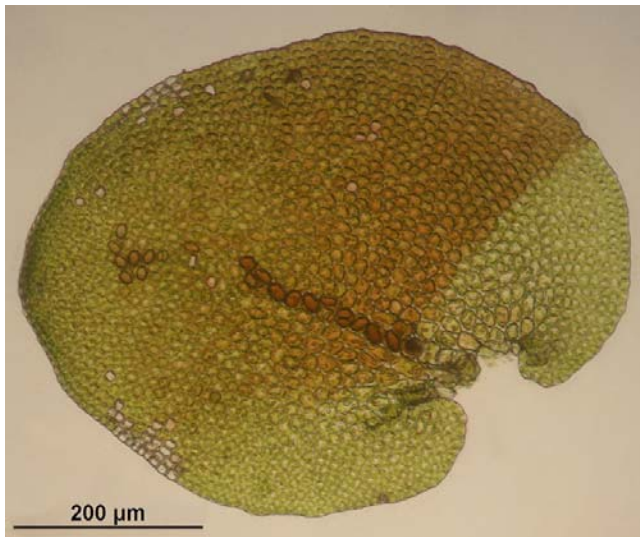


Figure 16. *Frullania tamarisci* with ocelli (row of brown cells). Photo by Hermann Schachner, through Creative Commons.



Figure 17. *Frullania* rhizoids. Photo courtesy of Andi Cairns.

Frey *et al.* (1990) suggested three principles of water conduction and storing mechanisms: draining surplus water, storing water in dry seasons, and condensing water vapor. They cited the "groovelike" arrangement of leaves as a mechanism to permit water support as well as drainage of water surplus. They found a significant correlation between water sacs (Figure 13), **mat** life form, and smooth bark in the epiphytic bryophyte communities of the lowland forest, facilitating water availability during short periods of dryness.

Parolly and Kürschner (2004) noted that the adaptive trends of functional types (life forms, life strategies, water conduction, and water storage) among the **oreal** (pertaining to mountains) trunk epiphytes at various elevations of southern Ecuador were distinct. They further concluded that these trends occur worldwide among tropical trunk epiphytes.

Kürschner (2003) conducted a phytosociological analysis on the epiphytic Afrotropical bryophytes of southwestern Arabia. These epiphytes are affected by monsoons, but at the same time must be drought-tolerant. *Orthotrichum diaphanum* (Figure 18) and *Syntrichia laevipila* (Figure 19) provide "character species" that define alliances. As in other studies, life forms and life strategies correlate with the ecological site conditions. The *Orthotricho* (Figure 18) – *Fabronietum socotranae* (see Figure 20) is a drought-tolerant, light-tolerant, and xerophytic alliance. It is dominated by cushions, short turfs, and mats of perennial stayers that regularly produce sporophytes. In contrast, the alliance in the shaded, subhumid habitats are described as the *Leptodonto* (Figure 21) – *Leucodontetum schweinfurthii* (see Figure 22) association. This association is comprised of **tail** or **fan**-forming **pleurocarpous perennial shuttles** that have large spores. This life strategy adapts them for short-range dispersal and moderately limited reproduction, with large spores more likely to survive and germinate than would smaller ones. Furthermore, this more humid atmosphere supports a much higher diversity in life forms and life strategies.



Figure 18. *Orthotrichum diaphanum*, member of a drought-tolerant, light-tolerant, and xerophytic alliance. Photo by Michael Lüth, with permission.



Figure 19. *Syntrichia laevipila* with capsules, a character species that defines an alliance of epiphytic Afromontane bryophytes in southwestern Arabia. Photo by Michael Luth, with permission.



Figure 20. *Fabronia pusilla*; *Fabronia* forms a drought-tolerant, light-tolerant, and xerophytic epiphytic alliance with species of *Orthotrichum* in Afromontane regions of southwestern Arabia. Photo by Michael Luth, with permission.



Figure 21. *Leptodon smithii*; *Leptodon* forms an epiphytic alliance with *Leucodon schweinfurthii* in the shaded, subhumid habitats of the Afromontane in southwestern Arabia. Note the **tail** or **fan-forming pleurocarpous** habit. Photo by Michael Luth, with permission.

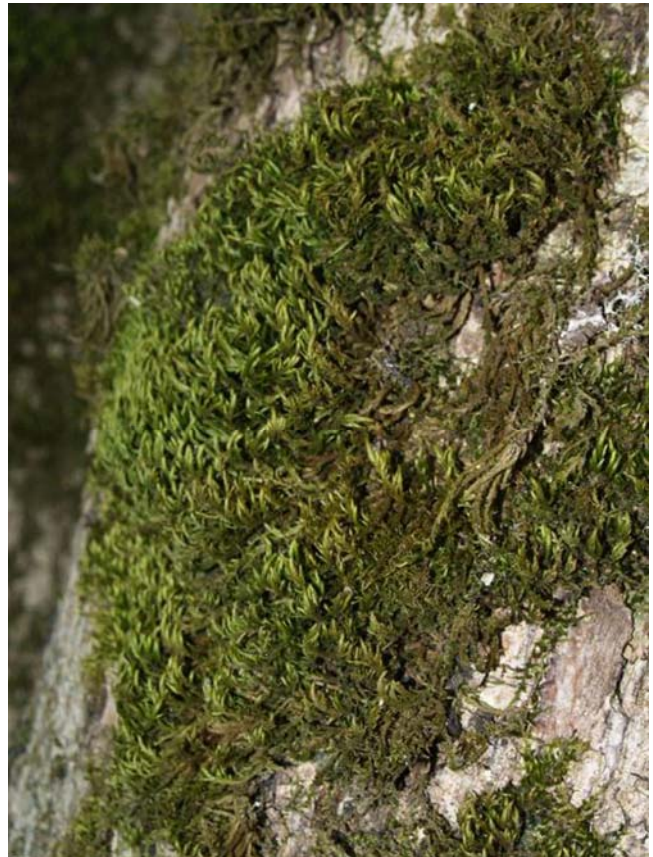


Figure 22. *Leucodon sciuroides*; *Leucodon schweinfurthii* forms an epiphytic alliance with *Leptodon* in the shaded, subhumid habitats of the Afromontane in southwestern Arabia. Photo from Elurikkus, through Creative Commons.

In a similar study on Socotra Island, Yemen, Kürschner (2004) described the epiphytic *Lejeuneo rhodesiae* (see Figure 23) – *Sematophylletum socotrensis* (see Figure 24) from the upper parts of Haghier Mountains. This association characterizes the evergreen Afromontane forests where heavy fogs and mists are typical. Kürschner identified three subassociations [*typicum*, *Hyophiletosum involutae* (drought-tolerant; Figure 25), and *Papillarietosum croceae* (shade-loving humid; Figure 26).

These subassociations are dependent on altitude, forest structure, life conditions, and humidity. Both the *typicum* and *Hyophiletosum involutae* subassociations are characterized by **perennial stayers** or **perennial shuttle** species that form **mats** and **short turfs**. They regularly produce sporophytes. The *Papillarietosum croceae* subassociation is likewise characterized by **perennial stayers** and **perennial shuttle** species that are **pendant** or **mat-forming**, but these have large spores with moderate-low reproductive rates. As seen in the more humid areas in the 2003 study, the *Papillarietosum croceae* subassociation has a much higher species richness with more diverse life forms and life strategies.



Figure 23. *Lejeunea* sp. growing as an epiphyll; *L. rhodesiae* forms an epiphytic alliance with *Sematophyllum socotrense* from the upper parts of Haghier Mountains, Yemen. Photo by Bramadi Arya, through Creative Commons.



Figure 24. *Sematophyllum substrumulosum*; *S. socotrense* forms an epiphytic alliance with *Lejeunea rhodesiae*. Photo by Johathan Sleath, with permission.

For a comparative discussion of life strategies in bryophytes as functional types, see Kürschner and Frey (2013). This treatise addresses vegetation types and their associated bryophyte life strategies for both temperate and tropical systems, based on more than 140 bryophyte communities and 1,300 taxa for corticolous, saxicolous, and terrestrial bryophytes. Sporn (2009) compared life

forms of bryophytes in various height zones in the forests of Central Sulawesi, Indonesia (Figure 27).



Figure 25. *Hyophila involuta*, in the drought-tolerant subassociation *Hyophiletosum involutae*, drying. Photo by Bob Klips, with permission.



Figure 26. *Papillaria croceae* in cloud forest – a species that prefers humid shade, found in the *Papillarietosum croceae* subassociation. Photo by Peter Woodard through Creative Commons.

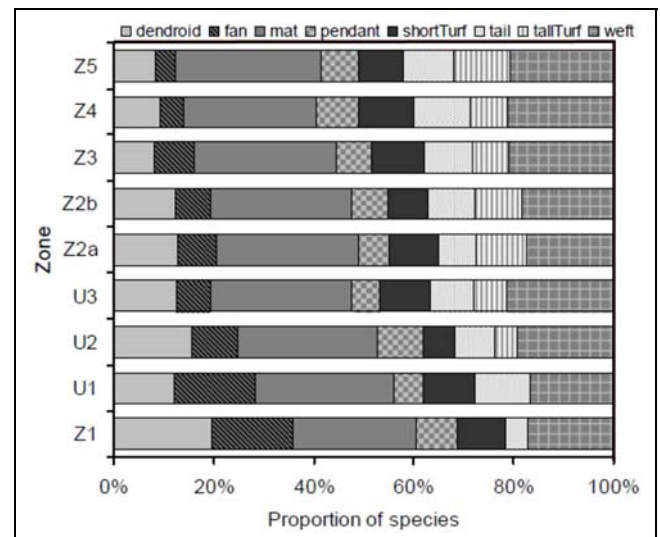


Figure 27. Comparison of eight life forms of bryophytes among five zones (Z1-Z5) of canopy trees and 3 zones of understory trees (U1-U3) in southwestern Nigeria. See Figure 28 for location of zones. From Sporn 2009.

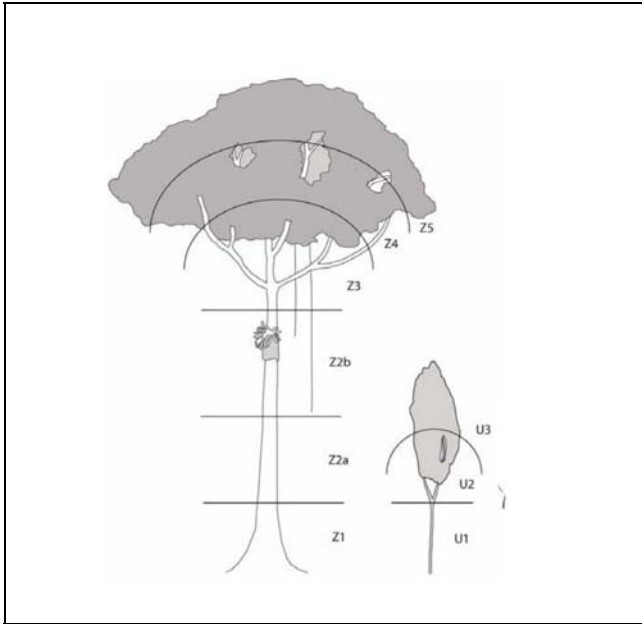


Figure 28. Epiphyte zones from Sporn 2009.

Osmotic Potential

Experimental studies on tropical bryophytes are still rare. However, several have looked at **osmotic potential**. This is the potential of water molecules to move from a **hypotonic** solution (more water, less solutes) to a **hypertonic** solution (less water, more solutes) across a semi permeable membrane. The osmotic potential becomes more negative as solutions become more concentrated.

Hosokawa and Kubota (1957) discussed the resistance to desiccation of epiphytic mosses from a beech forest in southwest Japan and related this to osmotic pressure. They found that the amount of time adult bryophytes could tolerate desiccation varied by species, but also by season of collection.

Akande (1984) looked at the use of **anhydrobiosis** (strategy that permits organisms to survive severe dry and/or extreme cold or hot conditions they often encounter) by corticolous tropical bryophytes as a means of surviving dry periods. Akande (1985b) also demonstrated the importance of **osmotic potential** (measure of tendency of solution with dissolved salts to withdraw water from pure water by osmosis, across differentially permeable membrane) as a factor in resistance to water stress in four Nigerian corticolous species. Using the mosses *Stereophyllum nitens* (see Figure 29-Figure 30) and *Calymperes palisotii* (Figure 31-Figure 32) and the leafy liverworts *Spruceanthus floreus* (syn. = *Mastigolejeunea florea*; see Figure 33) and *Frullania spongiosa* (see Figure 12) he found that the osmotic potentials of the corticolous mosses are higher than those of the tested liverworts. These osmotic potentials increase from wet to dry season. *Spruceanthus floreus* is less desiccation tolerant than the two mosses, but all three of these taxa could survive desiccation of 0%, 32%, and 54% relative humidities for six months at room temperature.



Figure 29. *Stereophyllum radiculosum*. In Nigeria, *Stereophyllum nitens* is a moss in which osmotic potential increases from wet to dry season. Photo by Juan David Parra, through Creative Commons.



Figure 30. *Stereophyllum nitens* herbarium specimen. Photo from Natural History Museum, London, through Creative Commons.



Figure 31. *Calymperes palisotii* on bark, a species with high osmotic potential. Photo by Scott Zona, through Creative Commons.

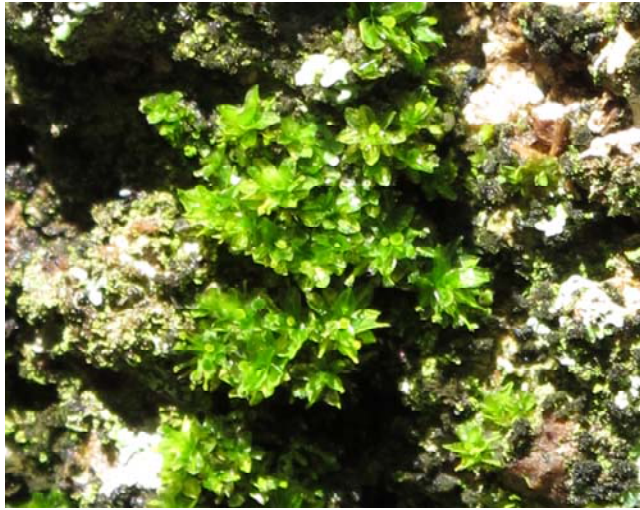


Figure 32. *Calymperes palisotii*, a species with high osmotic potential. Photo by Scott Zona, through Creative Commons.



Figure 33. *Spruceanthus planiusculus* in a genus where some of the tropical African species are less desiccation tolerant than mosses. *Spruceanthus floreus* has a demonstrated low osmotic potential. Photo by Claudine Ah-Peng, courtesy of Robbert Gradstein.

Proctor (2002) measured water relationships in two pendent mosses [*Pilotrichella ampullacea* (Figure 34), *Floribundaria floribunda* (Figure 35)] in Uganda. The estimated osmotic potential at full turgor in *P. ampullacea* was -1.82 MPa and in *F. floribunda* it was -1.43 MPa. Based on the definition above, net diffusion of water occurs from regions of less negative potential to ones of more negative (or lower) potential. Hence, in this case, more water would move into *P. ampullacea*. Both species are able to hold large quantities of external capillary water, up to ca. 12 in *P. ampullacea* and ca. 6 in *F. floribunda*. *Pilotrichella ampullacea* has a very rapid initial recovery (30-60 minutes after 20 h air drying at -37 MPa), but as desiccation time increased from 20 hours to 12 days recovery became less complete and full recovery time was slower. This osmotic relationship is well suited to its humid tropical forest environment. *Floribundaria floribunda* requires more continuously moist conditions.



Figure 34. *Pilotrichella ampullacea*, a species in Uganda that holds large quantities of external water. Photo by Jan-Peter Frahm, with permission.



Figure 35, *Floribundaria floribunda*, a species in Uganda that holds large quantities of external water, but requires nearly continuously moist conditions. Photo through Creative Commons.

Desiccation Recovery

One advantage that bryophytes have following desiccation is that liverworts and some mosses recover their full photosynthetic capacity within hours of rehydration, whereas resurrection ferns such as *Polypodium* (Figure 36) need at least a full day (Peterson *et al.* 1994). On the other hand, liverworts and most mosses lose water very quickly, whereas orchids, bromeliads, and other succulent tracheophytes lose water slowly. But some mosses also are able to retain their water for a longer time, as, for example, *Leucobryum* (Figure 37). *Leucobryum* has several adaptations that facilitate its water storage. It has a tight, compact cushion life form (Figure 37); its leaves are several cells thick (Figure 38); and it has **hyaline** (colorless – lacking chloroplasts; Figure 38) cells that permit water storage. Peterson and co-workers found that plants in the understory and gaps dried more slowly than did plants in their box treatment that simulated the canopy. Those in the gap dried slightly faster than did those in the understory.



Figure 36. *Polypodium polypodioides*, a resurrection fern that requires a full day to recover from desiccation. Photo by Korall, through Creative Commons.



Figure 37. *Leucobryum boninense*, showing the cushion life form. Photo by Tomio Yamaguchi, through Creative Commons.



Figure 38. *Leucobryum glaucum* leaf cells showing the outer hyaline cells surrounding the green chlorophyllous cells, typical of *Leucobryum* leaves. Photo by Walter Obermayer, with permission.

In French Guiana (Figure 39), 13 of 18 tested bryophyte species were able to maintain more than 75% of their photosynthetic capacity, as indicated by chlorophyll fluorescence, after 9 days of desiccation at 43% relative humidity (Pardow & Lakatos 2012). However, species from the understory required maintenance at 75% or higher relative humidity in order to recover. The researchers reactivated these bryophytes with water vapor only, a condition that is common in many tropical habitats, but which has been largely ignored in physiological ecology studies. The researchers concluded that tolerance to desiccation is of utmost importance as climatic changes occur (see also Wagner *et al.* 2013 and pertaining discussions in the subchapters on Tropics: Altitude).



Figure 39. French Guiana tropical forest. Photo by Cayambe, through Creative Commons.

Rainfall Interception

Frahm (2003a) compared the microhabitats of epiphytic bryophytes and lichens to determine why some trees were covered by lichens and others by bryophytes

(Figure 40) or others where lichens were in the crowns and bryophytes were on the trunks. Using humidity data loggers for one year, he used periods when the plants were wet and the relative humidity was at least 80%. He found that bryophytes typically thrive where there is a 20-30% longer duration of the wet period than where the lichens thrive. He cautioned that when doing pollution studies, such humidity differences should be considered.



Figure 40. Moss forest Mt. Ruwenzori Africa. Photo by G. Mieke, courtesy of Robbert Gradstein.

Pócs (1980) in the Uluguru Mountains, Tanzania (Figure 41), East Africa, examined the effect that epiphytic biomass (all kinds of epiphytes) had on the water balance of two rainforest types. With $2,130 \text{ kg ha}^{-1}$ dry matter in the submontane rainforest, the rain interception capacity was approximately $15,000 \text{ L ha}^{-1}$. By contrast, the mossy **elfin forest** (cloud forest; Figure 42) at 2,120 m altitude had approximately $14,000 \text{ kg ha}^{-1}$ with an interception capacity of $50,000 \text{ L ha}^{-1}$ during a single rainfall. Aerial humus accounts for a large portion of the interception capacity of the elfin forest, with ca $4,700 \text{ kg ha}^{-1}$ compared to ca 375 kg ha^{-1} in the submontane rainforest.



Figure 41. Uluguru Mountains, Tanzania. Photo by Aleksip, through Creative Commons.



Figure 42. Tanzania forest in fog. Photo by pxhere, through public domain.

Hölscher *et al.* (2004) examined the importance of epiphytes to rainfall interception in a tropical montane rainforest of Costa Rica. These canopy epiphyte masses are comprised mostly of mosses, liverworts, and lichens, all known for their ability to intercept rainfall. Biomass of all epiphytes was 1.9 t ha^{-1} dry weight in the studied 35-m-tall old-growth oak (*Quercus*) forest. The monthly moss water contents measured *in situ* ranged 24-406% of moss dry weight. This contrasts with sums of observed throughfall, stemflow, and interception measurements of 70, 2, and 28%, respectively, of the associated 2,150 mm of rain. Cloud water was not a factor in this ecosystem. This study suggested that mosses contributed only about 6% to the interception total, making the bryophytes much less important than in many rainforest ecosystems.

In central Veracruz, Mexico, Holwerda *et al.* (2010) assessed rainfall and cloud-water interception in a mature forest (Figure 43) and a 19-year-old secondary lower montane cloud forest. The researchers used separate calculations for events with rainfall only. They estimated cloud-water interception at 6% of dry-season rainfall (640 mm on average) for the secondary forest and 8% for the mature forest. On the other hand, annual values of cloudwater interception were less than 2% of the total rainfall (3,180 mm). The researchers considered the higher

loss in the mature forest to be the result of a higher canopy storage capacity, reflected in the greater tree leaf area and more epiphyte biomass.



Figure 43. Cloud forest, Bosque Comaltepec, Mexico. Photo by Prsjl, through Creative Commons.

In Colombia, Veneklaas and van Ek (1990) found that rainfall interception was 262 mm (12.4%) of the 2,115 mm of annual precipitation at 2,550 m elevation and 265 mm (18.3%) of the 1,453 mm precipitation at 3,370 m elevation. They found no evidence of fog precipitation. Most of this rainfall interception was accomplished by the epiphytic bryophytes. They attributed the higher rainfall retention at 3,370 m to differences in rainfall distribution and canopy storage capacities. They considered epiphytes to have an important role in this retention. The total epiphyte mass was approximately 12 tonnes (metric ton = 1,000 kg) dry weight per hectare, with most of it consisting of bryophytes and dead organic matter. In experiments, Veneklaas *et al.* (1990) found that epiphyte-covered branches were efficient in capturing rainfall. Most of this capture was accomplished by bryophytes. Release of this rainwater was very gradual, as was loss by evaporation.

In southeast Queensland, Ford (1994) found that epiphytes could absorb water 6-7 times their dry weight. This absorption affects stemflow and throughfall. The increased weight can cause outer, thin branches to break.

Other sources may prove helpful in understanding the water relations of tropical bryophytes. Pócs (1976) elaborated on the role of epiphytic bryophytes and other plants in the water balance of rainforests in the Uluguru Mountains, East Africa. Thompson *et al.* (1994) described the water-holding capacity of subtropical epiphytic bryophytes. Bergstrom and Tweedie (1995) described the hydrologic properties of epiphytic bryophytes. Kürschner and Parolly (1998b) described life forms and adaptations to water conduction and storage in North Peruvian epiphytic bryophytes. Other studies that pertain to rainfall interception are those of Kürschner & Parolly (2004) and Fleischbein *et al.* (2002).

Fog Interception

Some areas that receive little rainfall do experience fog on a regular basis (Lakatos *et al.* 2012). Fine wires and thin leaves are able to collect this fog water (Figure 44). Lakatos and coworkers measured dew formation on bark and lichens to be 0.29-0.69 mm d⁻¹. This water aids in cooling and provides enough moisture to prolong photosynthetic activity.



Figure 44. Spider web with fog drops; a similar appearance of water drops occurs on spider webs, fine wires, bryophyte leaf awns, and other thin structures in fog. For mosses, this is a source of water. Photo by Janice Glime.

Fog is able to provide sufficient water to many kinds of bryophytes in areas with low rainfall. Santon and Horn (2013) demonstrated this in lichens in a shrubland of northern Chile. They compared the ability to harvest fog water to the biomechanical mechanisms of filter-feeding aquatic invertebrates. Greater branchiness, as measured by fractal dimensionality, indicates greater fog-harvesting ability. Fractal dimension of the foliose and fruticose lichens increased significantly as fog availability increased.

Fog (Figure 45) is an important contributor to the cloud forest (elfin forest) (Camilo *et al.* 2008). The abundant epiphytes in these forests benefit from this fog input, especially during periods of lower rainfall. Camilo and coworkers suggested that it is especially important when wind speed is high and leaf water content has intermediate values, but that at both low and high leaf water content the interception of fog water is constrained.



Figure 45. Cloud forest showing fog, Ella, Sri Lanka. Photo by Kenny OMG, through Creative Commons.

In a subtropical montane forest in northern Taiwan, Chang *et al.* (2002) estimated fog deposition rate on epiphytic bryophytes by measuring the increase in plant weight when exposed to fog. Fog duration in this forest averaged 4.7 hours per day in summer months and 11.0 hours per day in other months. The maximum duration was 14.9 hours per day in November. The bryophytes experienced an average fog deposition rate of $0.63 \text{ g water g}^{-1} \text{ dw h}^{-1}$.

Many bryophytes in the cloud forest and some tropical rainforests are **pendent** (Figure 34-Figure 35). Renner (1932) referred to these as dripping liquid water under various conditions in Javanese forests. León-Vargas *et al.* (2006) demonstrated the humidity stratification in the lowland Amazonian forest in upper Orioco (Figure 46). They found that all six species of **pendent** bryophytes in their Venezuelan cloud forests could survive at least a few days of desiccation. High humidities supported more recovery than low humidities. They considered droplets of cloudwater to be important sources of water for **pendant** and other bryophyte life forms, particularly during periods of low rainfall.

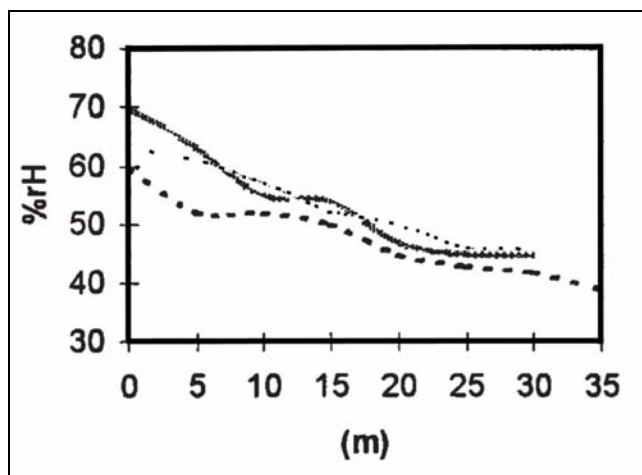


Figure 46. Relative humidity profile in meters above the ground in an Amazonian lowland forest of Surumoni, upper Orinoco. Modified from León-Vargas *et al.* 2006.

Pardow *et al.* (2012) described a recently discovered tropical lowland cloud forest type in the Guianas (Figure 47), originally discovered by Gradstein (2006) (see

Gradstein *et al.* 2010; Obregón *et al.* 2011; Gehrig-Downie *et al.* 2013). This habitat is created by frequent early morning fog events in the valleys, providing suitable habitat for a richer epiphytic species diversity compared to the common lowland rainforest. In the French Guiana (Figure 39) they compared the distribution of functional groups of epiphytes by height zone in the lowland cloud forest and lowland rainforest. These forests differed in composition of epiphytes in the canopy, especially in the mid and outer canopy, with the cloud forest exhibiting both a higher biomass and cover of both bryophytes and tracheophytes. Furthermore, the cloud forest had a richer bryophyte life-form composition. The cloud forest frequently exhibited tails, wefts, and pendants, life-forms that were nearly absent in the canopies of the common rainforest.



Figure 47. Canopy of a lowland cloud forest, French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Microclimate

In any ecosystem, a diversity of microclimates can increase the diversity of species. These provide differences in substrate, temperature, light, and moisture availability. With their many layers of canopy, the tropical forests provide a wide range of microclimates and niches.

One might expect that gradients in light and humidity would affect species diversity and richness. In a Brazilian Atlantic Forest remnant, Silva and Pôrto (2013) found the highest diversity and richness in the trunk zone. But they found no significant difference of bryophyte total richness or diversity along edge distance or vertical zonation gradients. However, at the species level, they found that shade epiphytes decreased significantly along vertical gradients, while sun epiphytes increased. They concluded that the bryophyte distribution in the forest is more related

to the microenvironmental gradation than to such landscape characteristics as edge distance.

Early studies by Biebl (1964, 1967) attempted to relate success of the tropical species to water and temperature. Wolf (1993a) recognized that some species from the Colombian lower montane rainforest were able to occupy the more exposed habitats in the warmer lowland rainforest of Guyana where they could receive more radiant energy. Furthermore, the epiphytes in the northern Andes tropical montane rainforests were divided by height on the tree, occupying a gradation of microhabitats characterized by differences in moisture (Figure 46) and light (Figure 48).

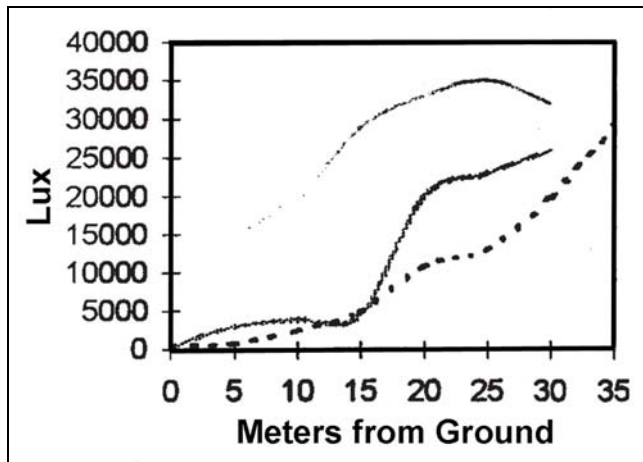


Figure 48. Light gradation from ground to canopy in an Amazonian lowland forest. Modified from León-Vargas 2001.

Temperature is one of the important aspects of microclimate. As noted by Wagner *et al.* (2013), bryophyte biomass and diversity both decrease dramatically as one goes from high to low altitudes in the tropics. They surmise that high respiration rates at high temperatures may at least in part explain this decrease. They transplanted two bryophyte species from 1,200 and 500 m asl to 500 m and sea level, respectively, in Panama and studied the short-term temperature acclimation of CO₂ exchange for 2.5 months. They also compared survival and growth for 21 months. Mortality was highest and growth lowest in transplanted samples, with no evidence of short-term acclimation.

Whereas the Wagner *et al.* (2013) study implies that temperature is important in altitudinal distribution of species, Wolf (1993c) suggests that it is a moisture gradient that accounts for epiphyte community differences in the northern Andes. Nevertheless, in a study in Panama, Zotz *et al.* (1997) found a strong diurnal variation in water content of tropical bryophytes in a lower montane rainforest. Both low and high water content limited carbon gain. More than half of the daily carbon gain was lost during the night as respiration, suggesting that temperature also was important.

Hosokawa and Odani (1957) tied the limits on the period of assimilation to the loss of carbon from respiration. They found that those species at the tree base (*Thuidium cymbifolium* (Figure 49), *Loeskeobryum cavifolium* (Figure 50), *Thamnobryum subseriatum* (Figure 51), *Homaliodendron scalpellifolium* (Figure 52) had a minimum light requirement of 400 lux, whereas those species higher in the trunk had a higher **light**

compensation point (light level at which photosynthetic gain = respiration loss on daily basis). On cloudy days, only the mosses at the tree base could reach their compensation point.



Figure 49. *Thuidium cymbifolium* with capsules, a tree base species with minimum light requirements. Photo by Li Zhang, with permission.



Figure 50. *Loeskeobryum cavifolium*, a tree base species with minimum light requirements. Photo by Digital Museum Hiroshima, with permission.



Figure 51. *Thamnobryum subseriatum*, a tree base species with minimum light requirements. Photo by Michael Luth, with permission.



Figure 52. *Homaliodendron scalpellifolium*, a tree base species with minimum light requirements. Photo by Taiwan Biodiversity, through Creative Commons.

The CO₂ levels differ throughout the canopy. In a subalpine forest of Taiwan, higher CO₂ levels occur in the lower canopy (Kao *et al.* 2000). Low CO₂ levels can limit photosynthesis, but higher levels can help to compensate for limited light.

Cao *et al.* (2005) found a correlation between epiphylls and light, moisture, habitat, and disturbance due to human activities. They found that the number of epiphytes increased from the center of the city to the outer suburbs. In the city, 67.4% of the epiphytes had a Levin's niche width of less than 0.1.

Gehrig-Downie *et al.* (2011) found that the lowland cloud forest had significantly more epiphytic biomass than did the lowland rainforest without fog in French Guiana (Figure 39). The lowland cloud forest is characterized by the high air humidity and morning fog that characterize river valleys in hilly areas, explaining the higher epiphytic bryophyte biomass.

Some of our understanding of microhabitat differences can be derived from studies on the effects of disturbance. For example, Werner and Gradstein (2009) conducted the first study comparing tracheophytic epiphytes and bryophytes along a disturbance gradient in a dry forest. They compared various degrees of disturbance in closed-canopy mixed acacia forest (old secondary), pure acacia forest (old secondary), forest edge, young semi-closed secondary woodland, and isolated trees in grassland (Figure 53). They found that density of bryophytic epiphytes on 100 trees of *Acacia macracantha* (in northern Ecuador; Figure 54) was significantly lower in edge habitat and on isolated trees than in closed forest. Forest edge was more impoverished than semi-closed woodland and had similar floristic affinity to isolated trees and to closed forest types. The microhabitats among these habitat types varied, contributing to the diversity. As they pointed out, "Assemblages were significantly nested; habitat types with major disturbance held only subsets of the closed forest assemblages, indicating a gradual reduction in niche availability." They found no diversity effect from distance to the forest for epiphytes on isolated trees. Species density was closely correlated with crown closure. They concluded that microclimate, not dispersal constraints, determined most of the epiphyte assemblage. Their most important conclusion is that in these dry environments, tracheophytic epiphyte diversity is not affected by disturbance, whereas bryophyte diversity is clearly affected. They attribute this to the poikilohydric

bryophyte condition that is more sensitive to changes in microclimate as compared to that of the homoiohydric tracheophytic epiphytes. The importance of microclimate for niche assembly of epiphytic bryophytes and absence of dispersal constraints is further supported by Oliveira *et al.* (2009) in the Guianas.



Figure 53. *Acacia koaia*. Degree of disturbance affects density of bryophytic epiphytes in forests of *Acacia macracantha*. Photo by Forest and Kim Starr, through Creative Commons.



Figure 54. *Acacia macracantha*, an Ecuadorian species with lower density of bryophytes at forest edges and on isolated trees. Photo by Vladeq, through Creative Commons.

Oliveira (2018) noted that the major differences from base to outer canopy are those of relative abundance. She then tested character traits of 104 species of epiphytic *Lejeuneaceae* (Figure 6, Figure 23) in the Amazonian terra firme forests. She examined dispersal ability, dark pigmentation of leaves, ability to convolute leaves when

drying, possession of thickened cell walls, monoicous vs dioicous reproduction, and facultative epiphyllous habit. Four of these six traits proved useful in separating canopy and/or understory communities. Interestingly, high dispersal ability did not vary much along the height gradient. She further noted that asexual propagules were not over-represented in the dynamic environment of the canopy, seemingly challenging the bryophyte life strategy theory.

Oliveira (2018) found that facultative epiphylls were over-represented on the tree bases. Dark pigmentation and convolute leaves were significantly more common in the canopy and less common at the base. These two traits can protect against high light intensity and prolong periods of hydration, respectively. The paucity of these species at the bases of trees may be the result of high temperatures and low light, made lower by the pigmentation, while the prolonged hydration in these conditions would add to a high rate of respiration relative to photosynthesis.

Stuntz *et al.* (2002) noted that microclimate goes two directions. Bryophytes not only respond to the microclimate around them, but they can have a major impact on the microclimate of the forest around them. To put it in the descriptive wording of the researchers, they "air-condition the forest."

Although their study included only two orchids and a bromeliad, Stuntz *et al.* (2002) showed that the space around these epiphytes had significantly lower temperatures than did areas of the same tree with no epiphytes. Evapotranspiration was reduced almost 20% compared to microsites with no epiphytes. This study would suggest that the effect of bryophytes on the microclimate in tropical forests could likewise be significant.

Understanding of the microclimate is important in management strategies if one wants to protect the bryophytes (Sporn 2009; Sporn *et al.* 2009). These researchers sampled understory trees in a natural forest and in two types (natural shade trees and planted shade trees) of *Theobroma cacao* (cacao; Figure 55) agroforests in Central Sulawesi, Indonesia. The two agroforests had low air humidity and high afternoon temperatures. Although bryophyte species richness differed little among the habitats, the species composition was markedly different between the natural forest and the agroforests. These differences were most likely the result of microclimate differences.

Nutrient Dynamics

Akande *et al.* (1985a) found that the nutrients in the tested corticolous bryophytes increased from the dry season to the wet season. The nutrient fluctuations were more pronounced in mosses than in the liverworts tested. They concluded that bryophytes must be significant in the nutrient cycling of tropical ecosystems.

We are beginning to understand now how bryophytes play a major role in nutrient dynamics in the tropical forest. Their ability to sequester rain and fog water consequently means that they can sequester the nutrients dissolved in this water. When they dry out, damaged membranes release the nutrients, and the early stages of precipitation dissolve these released nutrients and carry them downward.



Figure 55. Cacao plantation in Sulawesi, showing trunk epiphytes. Photo courtesy of Robbert Gradstein.

Vitousek (1984) summarized known nutrient relationships in lowland tropical forests, based on published studies from 62 tropical forests. He found that these forests and higher nitrogen levels lower ratios of dry mass to nitrogen in the litterfall compared to that ratio in most temperate forests. Nevertheless, the nitrogen return is comparable to that of temperate forests. Phosphorus return is very low in many of these tropical forests, whereas calcium return is high. The phosphorus cycling seems to be very efficient.

Sometimes the nutrients in the host affect the colonization by epiphytes. Benner (2011) found that epiphytes in the unfertilized Hawaiian montane forests (Figure 56) colonized high-phosphorus (fertilized) host trees more frequently than they did unfertilized trees. Mosses were less responsive to the fertilization than the cyanolichens. The cyanolichens were good predictors of chlorolichen and bryophyte abundance at three out of four Kauai, Hawaii, sites, indicating high bark and leaf phosphorus. Benner and Vitousek (2007) found that after 15 years of P fertilization in the forest, there was a "dramatic increase" in both abundance and species richness of the canopy epiphytes. There was, on the other hand, no response to fertilization with nitrogen or other nutrients.



Figure 56. Spring rainforest stream with mosses, Hawaii. Photo by Jcklyn Baltazar, through Creative Commons.

Nadkarni (1983, 1986) noted the importance of epiphytes in making a significant contribution to the overall nutrient cycling in both temperate forests and tropical rainforests. In both forest types they absorb nutrients collected from the atmosphere during the dry season. The net release from branches with epiphytes during the wet season is greater than that from branches stripped of their epiphytes. Chang *et al.* (2002) measured ion input in a subtropical montane forest in Taiwan and found that more than 50% of the ecosystem input arrived in fog deposition, suggesting that fog is an important nutrient contributor in some tropical ecosystems.

Nadkarni *et al.* (2004) found that the primary forest canopy of a cloud forest in Costa Rica had 63% of its organic matter as dead organic matter (DOM). Bryophytes comprised 12%. By contrast, the canopy organic matter of the secondary forest was 95% bryophytes, with only 3% DOM. Different locations within the primary canopy varied, with branch junctions having only dead organic matter and roots. Rather, bryophytes were the only organic matter at branch tips, subcanopy, and understory substrates. The trunks had diverse organic matter, but were dominated by tracheophytes and bryophytes; little dead organic matter was present. The secondary forest differed in having little difference in organic matter between trunks and branches. Canopy organic matter was high because of the strong presence of bryophytes. One surprise was that bryophytes were absent in branch junctions, although that is a likely place for them in other ecosystems. The researchers recommended transplant studies to try to determine the causes of the bryophyte distribution on the trees.

Rainfall vs Throughfall

Not all nutrients respond to their trip through the bryophyte sponges in the same way. Clark *et al.* (1998b) assessed net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. They found that phosphate, potassium, calcium, and magnesium were leached from the canopy, but nitrogen compounds were retained.

Hölscher *et al.* (2003) determined that differences in the canopy structure of predominately *Quercus copeyensis* (Figure 57) forests and epiphyte (mosses, liverworts, and lichens) abundance in old growth vs two ages of secondary growth in Cordillera Talamanca, Costa Rica, resulted in large differences in the way nutrient transport was divided into stemflow and throughfall. Nevertheless, the nutrient transfers reaching the soil were similar. Significantly higher litterfall of non-tracheophyte epiphytes indicated the higher epiphyte load in the old-growth forest.

In seeming contrast to the findings of Clark *et al.* (1998b), in a Venezuelan rainforest with a low-nutrient forest floor, the fluxes in calcium, sulfur, and phosphorus in the rainfall were greater than those in the throughfall (Jordan *et al.* 1980). Other elements occasionally had greater fluxes in the rainfall than in throughfall. Jordan and coworkers suggested that the canopy epiphylls (algae, lichens) intercepted and modulated the nutrients, resulting in their conservation in the canopy. Phosphate, potassium, calcium, and magnesium were at sometime later leached from the canopy. Seasonal data suggest that biomass burning increased concentrations of NO_3^- and NH_4^+ in cloud water and precipitation at the end of the dry season.

Regardless, a large majority of the inorganic N in atmospheric deposition was retained by the canopy at this site.



Figure 57. *Quercus copeyensis* with trunk epiphytes. Photo through Creative Commons.

To help us understand the effects the rainforest has on the nutrients, Wilcke *et al.* (2001) established five 20-m transects on the lower slope of a tropical lower montane rainforest in Ecuador. In the soil, they found the total Ca ($6.3\text{--}19.3\text{ mg kg}^{-1}$) and Mg concentrations ($1.4\text{--}5.4$) in the O horizon were significantly different between the transects. The throughfall ranged 43–91% of the rainfall; cloudwater inputs were less than 3.3 mm yr^{-1} except for one of the five transects where it was 203. Even the pH was affected by filtering through the canopy and associated epiphytes, increasing from a mean of 5.3 in the rainfall to 6.1–6.7 in the throughfall.

The leaves in this rainforest increase the element (Al, TOC, Ca, K, Mg) concentrations in the throughfall due to leaching from the leaves and washing off the dry deposition (TOC, Cu, Cl^- , $\text{NH}_4^+\text{-N}$) (Wilcke *et al.* 2001). This could be an advantage for inner canopy bryophytes that receive these nutrients from the top of the canopy. Only Mn, Na, and Zn escape enhancement as a result of throughfall contacts. However, in high flow events, even Mn and Zn are elevated in the throughfall.

The nutrient input to forest bryophytes is higher at 2,250 m than at 3,370 m asl in two montane tropical rainforests of Colombia (Veneklaas 1990) attributed this to the greater precipitation volume at the lower altitude. The losses of nutrients from the canopy were likewise higher at 2,550 m. Veneklaas considered the differences between forests to be related to differences in precipitation, geographical situation, and soil nutrient availability.

Bryophytes can alter the nutrient dynamics of the forest in a variety of ways. They act as sponges, absorbing rainfall, and with it the nutrients carried by that rainwater. Epiphytes furthermore trap water and nutrients as they flow down branches and tree boles, retaining nutrients leached from bark, leaves, and other kinds of epiphytes or collected in their dust. They host a variety of nitrogen-fixing bacteria, most notably the *Cyanobacteria* (Figure 58).



Figure 58. *Scytonema*, a genus that performs nitrogen fixation in the phyllosphere. Photo by Yuuji Tsukii, with permission.

Nitrogen Dynamics

Bergstrom and Tweedie (1998) found that epiphytes were able to access at least three sources of nitrogen, including atmospheric, the phorophyte through decomposed litter, and a source of nitrogen fixation. The ^{15}N exhibited considerable spatial heterogeneity within the tree.

Clark and coworkers (Clark 1994; Clark *et al.* 2005) reminded us of the large role bryophytes can have in nitrogen dynamics of a tropical forest. The assemblages of epiphytic bryophytes, vascular epiphytes, litter, and associated humus harbor ~80% of the inorganic nitrogen retained in the canopy (Clark 1994). The forest canopies are able to trap and retain inorganic nitrogen from rainfall, dry deposition of gasses, vapors, and particles, and nitrogen previously trapped by clouds. Because they form much of the surface area in the canopy and lack a thick cuticle (many, perhaps all, bryophytes have a waxy cuticle, but it is very thin) and epidermis, they are able to trap and retain this nutrient much more effectively than the tree leaves. Clark and coworkers compared nitrogen retention of field samples of epiphytic bryophytes, epiphytic assemblages, epiphytic tracheophyte foliage, and host tree foliage to cloud water and precipitation in a tropical montane forest canopy in Costa Rica. They estimated, using models and field data, that epiphytic bryophytes and epiphyte assemblages retained 33-67% of the nitrogen deposited by cloud water and precipitation. The model predicted an annual retention of 50% of the inorganic nitrogen that arrived through atmospheric deposition. The bryophytes are important in the transformation of inorganic nitrogen such as nitrates to less mobile forms such as ammonia, but also deposit some of it in **recalcitrant** (unresponsive to treatment; resistant, *i.e.*, it doesn't break down easily, if at all) forms of biomass, litter, and humus.

The collected nitrogen that is added to the epiphytic biomass, litter, and canopy humus (Vance & Nadkarni 1990, 1992) is eventually added to the very large pool of nitrogen in the soil organic matter (Edwards & Grubb 1977; Grieve *et al.* 1990; Bruijnzeel & Proctor 1995). Clark *et*

al. (1998b) found that the net nitrogen accumulation was ~8-13 kg ha⁻¹.

Cloud loadings can contribute to nutrient availability. Clark and Nadkarni (1992) experimented with excised epiphytes from Monteverde, Costa Rica, by subjecting them to NO_3^- loadings; from 0% to 90% of that NO_3^- is retained by the epiphytes. Ammonium (NH_4^+) is considerably more variable, ranging from a 200% loss to a 90% gain. These bryophytic epiphytes retain ca. 85% of the nitrate N from the atmospheric deposition to the canopy.

Wania *et al.* (2002) used ^{15}N levels to compare nitrogen in various positions within the forest canopy of a lowland rainforest in Costa Rica. The ^{15}N levels of canopy soils did not vary significantly, but the content in the epiphytes (including bryophytes) in different canopy layers did. The researchers concluded that epiphytes in different levels exhibited different ^{15}N during nitrogen acquisition.

Wanek and Pörtl (2008) examined nitrogen (NO_3^- , NH_4^+ , and glycine) uptake in bryophytes of a lowland rainforest of Costa Rica. They found no significant differences between the epiphyllous and epiphytic bryophytes. The mean uptake rates for these bryophytes are 1.8 $\mu\text{mol g}^{-1} \text{dw h}^{-1}$ for nitrate, 3.6 $\mu\text{mol g}^{-1} \text{dw h}^{-1}$ for ammonium, and 3.4 $\mu\text{mol g}^{-1} \text{dw h}^{-1}$ for glycine, suggesting that amino acids such as glycine significantly contribute to bryophyte nutrition in these epiphytes.

Most of the nitrogen fixation probably occurs on leaves with epiphylls. In any case, it is an important contributor to the tropical forest nitrogen dynamics. Matzek and Vitousek (2002) found that the total nitrogen fixation in a Hawaiian montane rainforest (Figure 59) was highest in sites having low N:P ratios in the leaves and stemwood. They suggested that epiphytic bryophytes and lichens depend on canopy leachate for their mineral nutrients, but the heterotrophic nitrogen fixation is controlled by the nutrient supply in the decomposing substrate. Differences in substrate cover had a larger effect on total N input from fixation than did fixation rates, a conclusion consistent with the low fixation rates observed in young forests. Nitrogen fixation in the **phyllosphere** (space surrounding a leaf) will be discussed under epiphylls.



Figure 59. Hawaiian tropical wet montane forest. Photo by Djzanni, through Creative Commons.

In 1998, Clark *et al.* (1998a) used epiphytic bryophyte samples in enclosures to estimate rates of growth, net production, and nitrogen (N) accumulation by shoots in the canopy in a tropical montane forest in Monteverde, Costa Rica. They also used litterbags to estimate rates of decomposition and N dynamics of epiphytic bryophyte litter in the canopy and on the forest floor. They estimated N accumulation at $1.8\text{--}3.0 \text{ g N m}^{-2} \text{ yr}^{-1}$. The cumulative mass loss from litterbags in the canopy after one year was $17\pm 2\%$ (mean ± 1 SE) and after two years $19\pm 2\%$ of initial sample mass. Mass loss from litter in litterbags after one year on the forest floor was $29\pm 2\%$, and from green shoots $45\pm 3\%$. On the forest floor, ca 47% of the initial N mass was lost within the first three months. The N that remained in the litter was apparently **recalcitrant** (resistant to microbial decomposition), although there was no evidence for net immobilization by either litter or green shoots. The annual net accumulation of N by epiphytic bryophytes was ca $0.8\text{--}1.3 \text{ g N m}^{-2} \text{ yr}^{-1}$.

Akande and coworkers (Akande 1985a; Akande *et al.* 1985) concluded that the role of bryophytes in nutrient cycling of African tropics is significant and requires study. Nutrient contents of bryophytes fluctuate with season, and in three forests at Ibadan, Nigeria, the highest mean monthly nutrient composition of the bryophytes is in June to July, with the lowest in November to January. Magnesium is an exception, reaching its peak in October when the other nutrients are diminishing. There are considerable differences between species, although the phenological patterns are very similar, with mosses accumulating more than liverworts. Relationships of bryophyte concentrations to those of bark suggest that the bryophyte obtains its nutrients from stemflow containing leachates not only from the canopy leaves, branches, and canopy dust, but also from the bark, and that bryophytes do not get nutrients directly from the bark, but rather get them only from those leached out by rain. Akande *et al.* concluded that the predominant source of these nutrients was from dust and other pollutants such as smoke and sulfur dioxide.

Base cation and fluxes increase in throughfall, but $\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$ decrease relative to that in rainfall in a subtropical montane moist forest in Yunnan, southwest China (Liu *et al.* 2002). The throughfall inputs of N, P, Ca, and S come primarily from precipitation, whereas most of the potassium and 2/3 of the magnesium in throughfall come from canopy leaching. The cycling rates for mineral elements are generally low compared to other tropical forests. Epiphytes are abundant on the bole and affect the chemical composition of the stemflow through selective uptake or release of elements. The total N, $\text{NH}_4^+\text{-N}$, Mg, Na, and $\text{SO}_4^{2-}\text{-S}$ are enhanced, while $\text{NO}_3^-\text{-N}$, K, P, and Ca are depleted in stemflow. Nitrogen from nitrogen-fixing organisms is low, most likely due to constraints by low temperatures.

In a study in the subtropical forest of northeastern Taiwan (Figure 60), Hsu *et al.* (2002) noted that nutrients in epiphytes and tree foliage are more readily available than those in the woody parts of the tree, making the tiny bryophytes proportionally more important than their size would suggest.

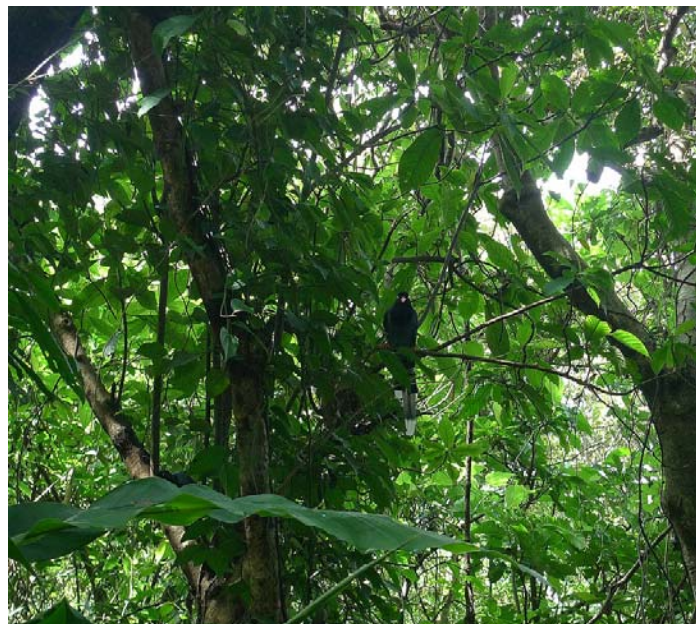


Figure 60. Taiwan blue magpie in subtropical rainforest of Taiwan. Photo by Gulumeemee, through Creative Commons.

Pulse Release

One mechanism by which the bryophytes help the forest floor plants is through pulse release of nutrients. This burst of nutrients occurs when dry bryophytes with damaged membranes first get water that wets them. This pulse is especially important for nutrients that are typically held in nutrient pools within the cells. The damaged membranes resulting from drying permits the rain to leach these nutrients from their otherwise safe interior locations. Coxson (1991) estimated the efflux of these solutes from stem segments of canopy bryophytes in tropical montane rainforest in Guadeloupe (Figure 61). These reached $80.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for potassium, $1.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for phosphorus, and $11.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for nitrogen in these rewetting episodes. On the other hand, estimates using intact bryophyte mats during natural field rewetting episodes were smaller, causing release of $28.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for potassium and $0.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for phosphorus. The lower numbers most likely result from internal recycling of released ions within the bryophyte mats.

Within the cloud forest canopy, and most likely elsewhere in the tropics, bryophytes accumulate considerable quantities of sugars (Coxson *et al.* 1992). In Guadeloupe, French West Indies (Figure 61), more than 950 kg ha^{-1} of sugars and polyols are released by epiphytic bryophytes per year as a result of wetting and drying cycles. The sugars come as a pulse during re-wetting, contributing to growth of the microbial flora both within and beneath the canopy. These sugars and polyols account for 17% of the dry weight of the upper canopy liverwort *Frullania atrata* (Figure 62), while providing less than 6% of the dry weight of the lower canopy moss *Phyllogonium fulgens* (Figure 63). (The name *Frullania atrata* may be incorrect as many species have incorrectly been identified as this one.)

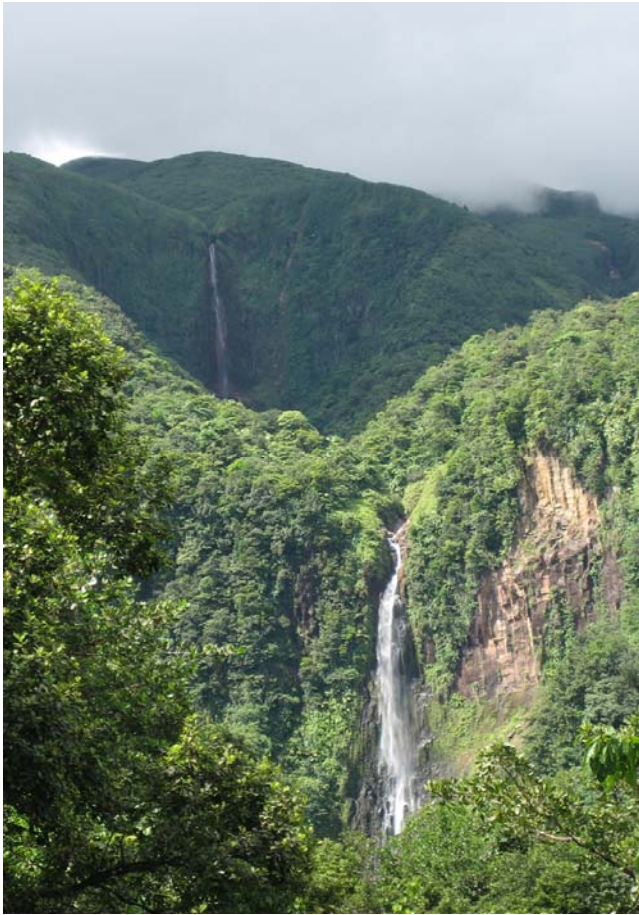


Figure 61. Montane rainforest, Guadeloupe. Photo by Bobyfume, through Creative Commons.

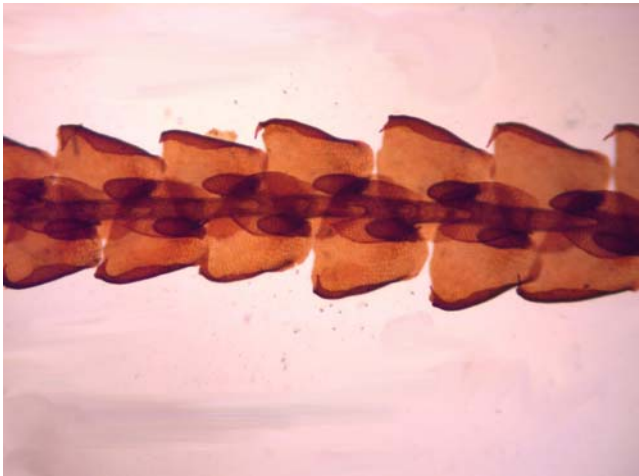


Figure 62. *Frullania atrata*, an upper canopy liverwort. Photo by Juan Larrain, with permission.

Keystone Resource

Nadkarni (1994a) attributed to the canopy epiphytes the role of **keystone** resource in the nutrient cycling of tropical forest ecosystems. That is, this is a resource that is critical to the structure and function of the ecosystem, without which the system would cease to function as it does. The epiphytic bryophytes may have a key role in the nutrient dynamics of these forests.



Figure 63. *Phyllogonium fulgens*, a lower canopy pendent moss. Photo by Yelitza Leon, Venezuelan Flora, through Creative Commons.

In a subtropical forest of the Ailao Mountains in Yunnan, southwest China, Liu *et al.* (2002) found that bryophytes enhance the annual amounts of total N, NH_4^+ -N, Mg, Na, and SO_4^{2-} -S but deplete NO_3^- -N, K, P, and Ca in the stemflow. Although many kinds of N-fixing organisms often are associated with epiphytic bryophytes, their contribution to total N in the mountains of Yunnan is most likely constrained by low temperatures. In a montane rainforest of the warmer Hawaii, on the other hand, Matzek and Vitousek (2003) found that the potential nitrogen fixation ranges from $\sim 0.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in a 300-year-old site to $\sim 1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in a 150,000-year-old site. They felt that the dependence of epiphytic bryophytes and lichens on nutrients leached from the canopy might account for the fact that the highest fixation rates occurred in sites with low N:P ratios in the leaves and stemwood of the trees. For heterotrophic fixation, the nutrient supply offered by the decomposing substrate is also important in controlling the fixation rate. Thus, older substrata with more epiphytes are likely to contribute more nutrients to these N fixers, and indeed Matzek and Vitousek did find that the fixation rates relate to substrate cover.

With an epiphyte biomass and associated soil of 44 tons ha^{-1} , the epiphytes form a significant contribution to the Colombian upper montane rainforests (Hofstede *et al.* 1993). The 20 kg of epiphytes exceeded the biomass of the

part of the tree that supported them. In this epiphytic community, the researchers found 2,360 g N, 215 g P, 1,350 g K, and 99 g Ca. The epiphytes create large accumulations of bryophytes, favored by low temperatures, continuous high humidity, low air turbulence, and the structure of the forest. The water-soluble phosphorus stored in the epiphytic biomass is higher than that of the forest floor soil.

Pentecost (1998) assessed the cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains of Uganda (Figure 64). He found that the lichens contain ~2% of the total above ground nutrients, whereas 8% occurs in the bryophytes. The concentrations of the three "fertilizer" nutrients were N (10 kg ha^{-1}), P (1 kg ha^{-1}), and K (3 kg ha^{-1}).



Figure 64. Rwenzori Mountains, western Uganda. Photo by Agripio, through Creative Commons.

Nadkarni (1984) reported 141.9 kg of epiphytes on a single *Clusia alata* (Figure 65) in a Costa Rican cloud forest. The nutrients in these epiphytes were estimated as 1062 g N, 97 g P, 678 g K, 460 g Ca, 126 g Mg, and 207 g Na. This is significant because this relatively small component (less than 2%) of the forest biomass holds up to 45% of the nutrients found in the foliage of similar forests and stresses the importance of epiphytes as keystone resources in the nutrient dynamics of these forests.

Canopy Roots

To me, the most intriguing relationship is the relationship of bryophytes with canopy roots, first discovered and described by Nalini Nadkarni in her classical paper in *Science* (1981). Laman (1995) reported the improved germination of *Ficus stupenda* in moss beds associated with canopy knotholes, attributing their survival to good moisture retention. However, seed harvesting ants (*Pheidole* sp.; Figure 66) killed many of the seedlings later in development.



Figure 65. *Clusia alata*, a common epiphyte host in Costa Rica. Photo by Evaristo Garcia Foundation, through Creative Commons.



Figure 66. *Pheidole pilifera* minor (left) and major (right) workers. Some species of *Pheidole* kill *Ficus stupenda* seedlings in epiphytic moss beds. Photo by M. L. Muscedere and J. F. A. Traniello, through Creative Commons.

Epiphytic bryophytes also provide a rooting medium for **adventitious roots** (roots that arise from stem tissue; Figure 67) of trees. In fact, a dynamic interaction may occur in which the bryophytes help the tree, and the tree roots likewise help the establishment of the epiphytic community (Nadkarni 1994b). The bryophyte mat traps inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson *et al.* 1992) that are leached from members of the epiphyte community. These nutrients nourish the roots of the tree (Nadkarni & Primack 1989). The two appear to grow in mutual benefit, with the roots benefitting from the nutrients and providing a larger anchoring system for the epiphytes as they grow (Nadkarni 1994b). As the bryophytes and organic matter increase, they provide more leachates, causing the tree roots to increase.



Figure 67. Adventitious roots of banyan tree (*Ficus benghalensis*). Photo through Creative Commons.

Nadkarni (1981) found that epiphytes, including bryophytes, stimulate the growth of adventitious roots. The bryophytes serve to trap nutrients for them, and the relationship is so strong that Nadkarni argues that evolution has selected for it.

In *Senecio cooperi* (Figure 68), a species in the tropical cloud forest, Nadkarni (1994b) experimented with epiphytes air-layered on stem segments. For comparisons, she used wet epiphytes or dry epiphytes plus associated humus, sponges wetted with either water or nutrient solutions, dry sponges, and controls with no added layering. The wet epiphyte-humus mix and sponges with nutrient solutions were most successful in producing roots. Nadkarni suggested that the epiphytes intercept nutrients that they retain and provide the "cue" for the host tissue to produce the roots.

Some adventitious roots take advantage of the microenvironment created by epiphytic bryophytes (Sanford 1987). The roots are able to grow upward, and can do this in as rapidly as 5.6 cm in 72 hours. The roots are less than 2 mm in diameter and grow on the exposed bark surfaces, in bark fissures, and beneath attached epiphytic mosses, ferns, and vines.

Epiphytes decompose in the canopy to form soil on the large branches (Hietz *et al.* 2002). Epiphyte groups differ, in part relating to uptake of N through mycorrhizae or nitrogen fixation. These different sources affect the highly

variable quantity of epiphytes, often depending on the systematic group and canopy position.



Figure 68. *Senecio cooperi*, a species that produces aerial roots in wet epiphytes. Photo by Dick Culbert, through Creative Commons.

In Hawaii, the koa tree (*Acacia koa*; Figure 69) takes advantage of the bryophyte mats for moisture and other favorable conditions (Leary *et al.* 2004). The roots of this tree actually grow upward and form **nodules** (Figure 70) with the bacterium *Bradyrhizobium* (Figure 71) in pockets of organic soils within the canopy. These organic soils in the tree contain significantly higher levels of exchangeable cations and total nitrogen, and significantly lower aluminum levels than the ground soils. Some of these mats have significant bryophyte presence.



Figure 69. *Acacia koa*, Maui, Hawaii, a species that forms adventitious roots in moss clumps on the trunk. Photo by Forest and Kim Starr, through Creative Commons.



Figure 70. *Acacia koa* nodules in a bed of mosses. Photo courtesy of Leary *et al.* 2004.

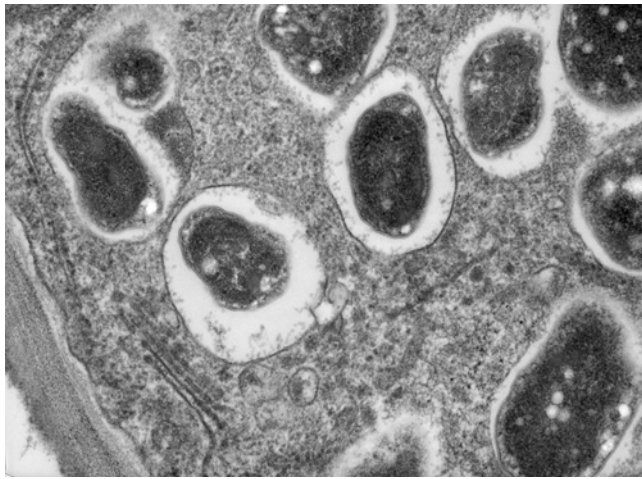


Figure 71. *Bradyrhizobium* from root nodule. Photo by Louisa Howard, through public domain.

Herwitz (1991) examined the aboveground adventitious roots of *Ceratopetalum virchowii* (see Figure 72) in an Australian montane tropical rainforest. These roots developed from stems and branches of this canopy species. In this case, Herwitz could find no evidence that this tree requires the epiphyte mats to stimulate its root growth. Instead, it appears that the stemflow of this species is particularly rich in Ca^{2+} , Mg^{2+} , and Na^+ compared to the soil. The bark of this species remains moist for a long period of time, providing a suitable environment for the adventitious root.

Productivity and Biomass

Studies on productivity in the tropics are rare. Jacobsen (1978) published one of the earliest studies. Most seem to be simply reports of standing crops. Several look at the effects of temperature on net carbon storage (see above under Microclimate).

Köhler *et al.* (2007) reported that bryophytes dominate the epiphytic vegetation in both an old-growth cloud forest and a 30-year-old secondary forest on slopes of the Cordillera in northern Costa Rica. The combined epiphyte biomass and canopy humus was $16,215 \text{ kg ha}^{-1}$ in the old-growth forest and $1,035 \text{ kg ha}^{-1}$ in the secondary forest.



Figure 72. *Ceratopetalum apetalum*; *C. virchowii* forms adventitious roots but shows no evidence of influence by epiphytic bryophyte mats. Photo by John Tann, through Creative Commons.

Van Dunne and Kappelle (1998) studied epiphytic bryophytes on five small stems of *Quercus copeyensis* (Figure 57) in a Costa Rican montane cloud forest (Figure 73). They found 22 species of mosses and 22 species of liverworts. Biomass of the bryophytes correlates with their frequency, with bryophytes contributing 54-99% of the biomass. Nearly 90% of the biomass is contributed by only 14% of the species, with the predominant contributors being the mosses *Pilotrichella flexilis* (Figure 10), *Rigodium* sp. (Figure 74), *Porotrichodendron superbum* (Figure 75), *Prionodon densus* (Figure 76), *Neckera chilensis* (see Figure 77), and the leafy liverwort *Plagiochila* (Figure 78).



Figure 73. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.

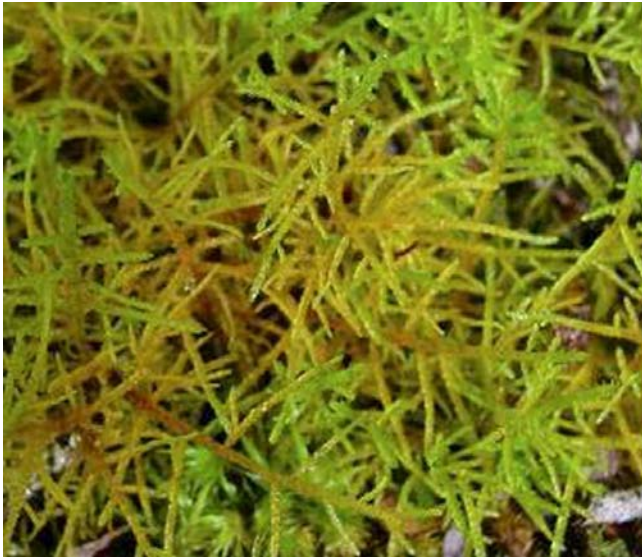


Figure 74. *Rigodium pseudo-thuidium*, in a genus that is a major biomass contributor to Costa Rican epiphytes. Photo by Juan Larrain, with permission.



Figure 77. *Neckera scabridens*; *N. chilensis* is a major biomass contributor to Costa Rican epiphytes. Photo by Juan Larrain, with permission.



Figure 75. *Porotrichodendron superbum* with capsules, a species that is a major biomass contributor to Costa Rican epiphytes. Photo Paris Cryptogamic Herbarium, through Creative Commons.



Figure 78. *Plagiochila* sp., in a genus that is a major biomass contributor to Costa Rican epiphytes. Photo by Jan-Peter Frahm, with permission.



Figure 76. *Prionodon densus*, a major biomass contributor to Costa Rican epiphytes. Photo by E. Lavocat Bernard, with permission.

Frahm (1987) raised the question of how altitude affected the biomass and productivity of epiphytes in the tropics. Researchers had typically assumed that it related to greater light and lower temperatures at higher altitudes, permitting greater photosynthesis, but no physiological studies had been used to support this hypothesis. In his study, he used a transect with sampling at 200-m intervals from 200 to 3,200 m asl in Peru. He determined biomass in the field and measured CO₂ gas exchange in a series of light and temperature combinations in the lab. The lab experiments used specimens from 2,300 m asl collected in Colombia in October. These were 150 cm² specimens of the mosses *Neckera* sp. (Figure 77), *Heterophyllum affine* (Figure 79), *Porotrichum* sp. (Figure 80), and the liverwort *Metzgeria* (Figure 81). These experiments support the

hypothesis that it is a combination of high temperatures and low light that limits most of these tropical bryophytes at lower elevations. They are unable to store enough carbon in the low light to balance that lost to respiration at the high temperatures of the lowland forest. This is supported by experiments with temperature on the moss *Plagiomnium rhynchophorum* (Figure 82-Figure 83), but unfortunately, no methods were provided.



Figure 79. *Heterophyllum affine*, a species in which high temperatures and low light limits these tropical bryophytes. Photo by Blanka Shaw, with permission.



Figure 80. *Porotrichum bigelovii*; a species in this genus has high temperature and low light limits in tropical habitats. Photo by Ken-ichi Ueda, with online permission.



Figure 81. *Metzgeria*, a genus that has high temperature and low light limits in tropical habitats. Photo by Michael Lüth, with permission.



Figure 82. *Plagiomnium rhynchophorum* with capsules, a mostly Asian tropical moss that has no net photosynthetic gain at 25°C and above. Photo by Germaine A. Parada, through Creative Commons.

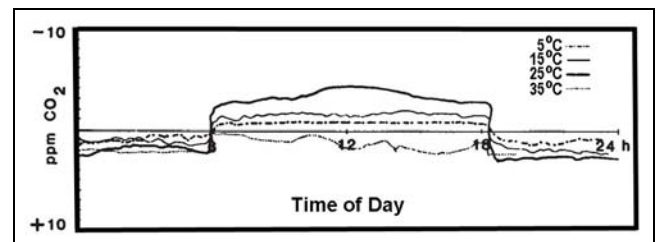


Figure 83. Photosynthesis of *Plagiomnium rhynchophorum* (Figure 82) under various temperature conditions at 1500 lux. The montane forest conditions of 5° and 15°C yield sufficient net photosynthesis; the lowland condition of 25°C permits photosynthesis throughout the day but no net photosynthetic gain. At 35°C no net photosynthesis occurs during the day. Graph modified from Frahm 2003b.

Wolf (1993b) found that altitude explains most of the variation in the epiphytic bryophytes and lichens on selected bark types of canopy trees, using 15 sites on an altitudinal transect from 1,000 to 4,130 m asl in the Central Cordillera of Colombia (Figure 84). Species richness varies among the three groups (mosses, liverworts, and lichens). Liverworts reach their greatest species richness (ca 100 taxa) at mid-elevational sites (2,550-3,190 m asl). In this case, biomass of bryophytes and lichens increases with altitude, coinciding with an increase in humidity.



Figure 84. Cordillera in central Colombia. Photo by Samuel Rengifo, through Creative Commons.

Hofstede *et al.* (1993) examined the relationship between the epiphytic biomass and the nutrient status in a Colombian upper montane forest near the treeline at 3,700 m asl with a massive presence of epiphytes. The amount of accumulated epiphytic mass, suspended soil, and living plants on a full-grown tree was 32.7 g dry weight per dm² surface area, the highest documented value ever. This high value is attributed to a combination of low temperatures, high humidity, low wind velocities, and structural characteristics of the tree.

Müller and Frahm (1998) sampled epiphytic bryophytes in a montane rainforest in the Andes of Ecuador at about 2,000 m asl. They measured the dry weight on various parts of the trees and found that on trunks it was 80 g m⁻², on branches 1,873 g m⁻², and on twigs 1,230 g m⁻².

Clark *et al.* (1998a) conducted one of the few studies on retention of carbon by the tropical epiphytic bryophytes. They found an annual net accumulation of carbon to be approximately 37-64 g C m⁻² yr⁻¹ in their study in a tropical montane forest in Monteverde, Costa Rica. Net production of epiphytic bryophytes in the forest was 122-203 g m⁻² yr⁻¹.

In the upper montane forest of the Rwenzori Mountains of Uganda, Pentecost (1998) found that large cushion-forming liverworts are dominant in the lower canopy. These are predominately *Chandonanthus* (Figure 85), *Herbertus* (Figure 86-Figure 87), and *Plagiochila* (Figure 88) species. Their productivity is controlled by light intensity and substrate tree age. In total, he found 14 species of bryophytic epiphytes. The total epiphytic biomass, including bryophytes, lichens, and algae, contribute nearly 1 ton ha⁻¹ standing crop, a figure that is approximately 10% of the above-ground standing crop.



Figure 85. *Chandonanthus birmensis*, in a genus that forms large cushions in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Manju Nair, through Creative Commons.



Figure 86. *Herbertus aduncus* in BC, showing large "muffs" around branches. This genus forms large cushions in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Botany Website, UBC, with permission.



Figure 87. *Herbertus aduncus* showing dense cushions formed by this genus in the lower canopy of the Rwenzori Mountains of Uganda. Photo from Botany Website, UBC, with permission.



Figure 88. *Plagiochila cristata* showing dense cushions like those formed by other members of this genus in the lower canopy of the Rwenzori Mountains of Uganda. Photo by Michael Lüth, with permission.

Lösch *et al.* (1994) describe differences in environmental conditions and photosynthetic rates for bryophytes in a rainforest (800 m asl), a bamboo forest, and a tree-heath (2,200-3,200 m asl) in east central Africa. In the lowland rainforest, the climatic conditions are a nearly constant 24°C, 100% relative humidity, and PAR below 100 $\mu\text{mol photons m}^{-2} \text{ sec}^{-1}$. The mountain bryophytes exhibit approximately 6 times those daily sums of PAR while experiencing temperatures of 10-25°C and relative humidities of 60-100%. In the bamboo forest, the epiphytic mosses experience water loss down to less than 70% of their water content, but become saturated again from the vapor-saturated air at night. In these habitats, the photosynthesis peaks between 22 and 30°C. The lowland species exhibit higher optima than do those of the mountain sites. The light saturation points for all species are below 400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, but the slopes differ. Those bryophytes from the lowland have a smaller light compensation point (3-12 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$), accompanied by a steeper slope in the low-light range. In the highland, the compensation point is 8-20 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$.

Waite and Sack (2010) considered the relationship of moss photosynthesis to leaf and canopy structure. These include ground-dwelling species as well as branch and trunk dwellers: *Acroporium fuscoflavum* (Figure 89), *Campylopus hawaiiicus* (Figure 90), *Distichophyllum freycinetii* (Figure 91), *Fissidens pacificus* (Figure 92), *Holomitrium seticalycinum* (see Figure 93), *Hookeria acutifolia* (Figure 94), *Leucobryum cf. seemannii* (Figure 95), *Macromitrium microstomum* (Figure 96), *M. piliferum* (Figure 97), and *Pyrrhobryum pungens* (see Figure 98) (all mosses). Interestingly, they did not find any correlation between light saturation for photosynthesis and habitat irradiance. The bryophytes have low leaf mass per area and a low gas exchange rate. The nitrogen concentration, as well as A_{mass} , (maximum assimilation per unit leaf mass) has a negative correlation with the canopy mass per area. *Campylopus pyriformis* (Figure 99) exhibits a high A_{max} (maximum assimilation) that could be the result of its high leaf area index. Anatomical factors such as smaller cells, thicker cell walls, or physiological adaptations such as higher osmotic adjustment could lower the potential for a higher A_{max} in sun mosses.



Figure 89. *Acroporium fuscoflavum*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.



Figure 90. *Campylopus hawaiiicus*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.



Figure 91. *Distichophyllum freycinetii*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by John Game, through Creative Commons.



Figure 92. *Fissidens pacificus*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.



Figure 93. *Holomitrium trichopodum*; *Holomitrium seticalycinum* is a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Niels Klazenga, with permission.



Figure 94. *Hookeria acutifolia*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Michael Lüth, with permission.



Figure 95. *Leucobryum seemannii*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.

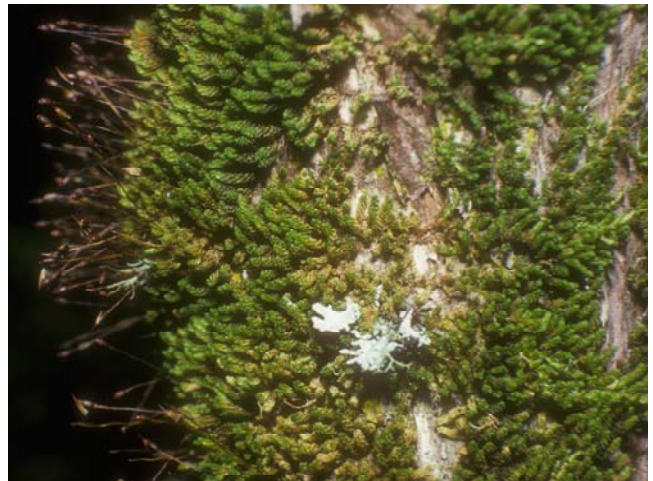


Figure 96. *Macromitrium microstomum*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Janice Glime.



Figure 97. *Macromitrium piliferum*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Jan-Peter Frahm, with permission.



Figure 98. *Pyrrhobryum* sp.; *Pyrrhobryum pungens* is a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Niels Klazenga, with permission.



Figure 99. *Campylopus pyriformis*, a moss for which there is no correlation between light saturation for photosynthesis and habitat irradiance. Photo by Michael Lüth, with permission.

Epiphyte Litterfall

Both bryophyte and tracheophyte litter can fall from the trees, especially during severe storms. This is a loss of canopy productivity, but provides a new source of nutrients for the soil, and in some cases these plants may continue growth on the ground.

Matelson *et al.* (1993) considered the rate of nutrient release from bryophytic and other epiphytic litter fall. They determined that it varies with microhabitat and suggested that both spatial and temporal distribution should be studied at the species level as they relate to microhabitat characteristics.

Köhler (2002) investigated total epiphytes in 10-15-year-old early secondary forest, a 40-year-old later-stage secondary forest, and an old-growth (primary) forest in Costa Rican mountain rainforests. Succession resulted in an increase in epiphytic litterfall. They estimated 4.8 g m^{-2} in early secondary forests (160 kg ha^{-1} at stand level), 12.0 g m^{-2} in later secondary forest (520 kg ha^{-1} at stand level), and 78.5 g m^{-2} in the old-growth forest (3400 kg ha^{-1} at stand level). Nevertheless, epiphytes constitute only a small part of the litter.

In a Neotropical cloud forest in Monteverde (Figure 100), Costa Rica, Nadkarni and Matelson (1992) found that epiphyte litter (bryophytes, lichens, and tracheophytes) comprises 5-10% of the total fine litter at that site. This litterfall contributes to the nutrients of the forest, with measurements (in $\text{kg ha}^{-1} \text{ yr}^{-1}$) of N (7.5), P (0.5), Ca (4.2), Mg (0.8), and K (0.1). These epiphytic litter components have a higher annual rate than does the litter from plants rooted in the ground. On the other hand, the turnover time of all nutrients except potassium is 4-6 times slower in the fallen epiphytic litter. Potassium turnover is ten times as fast. In a later study, Nadkarni (2000) determined that epiphyte litterfall in a lower montane cloud forest in Monteverde, Costa Rica, occurs at a rate of $50 \text{ g dry wt m}^{-2} \text{ yr}^{-1}$. This slow turnover of most bryophyte litter is most likely due to the high phenolic content that protects the bryophytes from herbivory and attack by fungi and bacteria.

When branches make contact with each other, by wind or storm, the impact can cause tiny branches at the tips to break, a phenomenon known as **crown shyness** (Figure 101) (Franco 1986). This can occur between the same species of tree, or among different species. The exact cause is not clearly known, but at least in some cases it appears that it is the result of **reciprocal pruning** as trees contact each other. It appears that lateral branch growth is usually not influenced by the neighbors until such mechanical abrasions occur. One such tree is *Clusia alata* (Figure 65). This branch breakage can cause any adhering bryophytes to be lost from the canopy as the branch tips fall away.



Figure 100. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.



Figure 101. Crown shyness in Buenos Aires, Argentina; branches break when they contact in wind events. Refractor, through Creative Commons.

Summary

Bryophytes in the tropics, particularly epiphytes, undoubtedly have a crucial role in water and nutrient retention, releasing nutrients during re-wetting, but filtering them from the lower branches and ground during rain events. They are adapted by their life forms and physiology to withstand desiccation. **Anhydrobiosis** and **osmotic potential** are typically used as means of surviving dry periods. Dry areas typically have **mats**; in areas with high humidity these are replaced by **fans**, **wefts**, and **pendants** that are able to obtain water from fog and mist (**fog-stripping**). Many are **perennial stayers** or **perennial shuttle** species.

Species of highly exposed locations have higher light saturation and compensation points, higher dark respiration rates, more chlorophyll, higher chlorophyll *a:b* ratios, and higher N concentrations than those of shade species. Some are able to retain water and nutrients in **hyaline** cells that hold water and surround photosynthetic cells. But most lose water easily and survive by their ability to recover quickly from desiccation, without the need to make new chlorophyll.

Substrate, temperature, light, and moisture availability are the microclimate variables that drive the community structure of epiphytic bryophytes. Their biggest physiological problem is the need to store more carbon than they lose to respiration.

Nutrients are obtained from the atmosphere, rain, and the bark and collected on the bryophyte surface until it becomes moist and can absorb them. Hence, nutrients in the bryophytes increase from the dry season to the wet season. **Cyanobacteria** living in the microenvironment of the bryophytes contribute to the usable nitrogen of the ecosystem. The ability of the bryophytes to leak nutrients but retain them on their surfaces permits external nutrient storage until rainfall returns, but releases them to the ecosystem as heavy rains carry them away. Light rains and fog permit the bryophytes to hydrate and absorb the nutrients. This makes the epiphytic bryophytes a keystone resource for the forest. These nutrient-rich, wet bryophytes furthermore provide a suitable substrate for canopy roots for some species.

Biomass of the bryophytes correlates with their frequency, with bryophytes contributing 54-99% of the biomass at higher elevations. Biomass increases with altitude, coinciding with an increase in humidity. At lower elevations, the combination of high temperatures and low light severely limit bryophyte productivity. Epiphyte litter (bryophytes, lichens, and tracheophytes) comprises 5-10% of the total fine litter in the cloud forests and only a small amount in the lowland forest. Whereas leaf litter decays rapidly in the tropics, bryophyte litter is slow to decay due to its many phenolic compounds that inhibit insects, bacteria, and fungi.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make a very early version of this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about. S. Robbert Gradstein reviewed this subchapter for accuracy and suggested references to add. Michael Lüth generously permitted my use of his beautiful images for this and other subchapters.

Literature Cited

- Akande, A. O. 1984. Anhydrobiosis in corticolous bryophytes. *Trop. Ecol.* 25: 255-259.
- Akande, A. O. 1985a. Nutrient studies of some corticolous bryophytes in Nigeria. *Cryptog. Bryol. Lichénol.* 6: 121-133.
- Akande, A. O. 1985b. Osmotic potential – A factor for resistance to water stress in some Nigerian species of corticolous bryophytes. *Trop. Ecol.* 26: 80-84.
- Akande, A. O., Olarinmoye, S. O., and Egunyomi, A. 1985. Nutrient studies of some corticolous bryophytes in Nigeria. *Cryptog. Bryol. Lichénol.* 6: 121-133.
- Akiyama, H., Yamaguchi, T., and Suleiman, M. 2001. The bryophyte flora of Kinabalu National Park (Sabah, Malaysia), based on the collections by Japan-Malaysia collaborative expeditions in 1997. *Nat. Human Activ.* 6: 83-99.
- Ando, H. 1969. Epiphytic bryophytes on *Buxus microphylla* var. *insularis* growing on limestone ridges in Taishaku. *Hikobia* 5: 177-178.
- Barkman, J. J. 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes*. Van Gorcum & Co., Assen, Netherlands, 628 pp.
- Benner, J. W. 2011. Epiphytes preferentially colonize high-phosphorus host trees in unfertilized Hawaiian montane forests. *Bryologist* 114: 335-345.
- Benner, J. W. and Vitousek, P. M. 2007. Development of a diverse epiphyte community in response to phosphorus fertilization. *Ecol. Lett.* 2007: 628-636.
- Bergstrom, D. M. and Tweedie, C. E. 1995. Hydrological properties of epiphytic bryophytes in a subtropical Australian rainforest. In: *International Association of Bryologists. Proceedings of the International Bryological Conference. Tropical Bryophytes: Biology, Diversity and Conservation*, Mexico City, 7-12 August 1995, pp. 18-19.
- Bergstrom, D. M. and Tweedie, C. E. 1998. A conceptual model for integrative studies of epiphytes: Nitrogen utilisation, a case study. *Austral. J. Bot.* 46: 273-280.
- Biebl, R. 1964. Austrocknungsresistenz tropischer Urwaldmoose auf Puerto Rico. [Drying resistance of tropical jungle moss in Puerto Rico.]. *Protoplasma* 59: 277-297.
- Biebl, R. 1967. Temperaturreistenz tropischer Urwaldmoose. [Temperature resistance of tropical jungle moss.]. *Flora* 157: 25-30.
- Bruijnzeel, L. A. and Proctor, J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? In: Hamilton, L. S., Juvik, J. O., and Scatena, F. N. (eds.). *Tropical Montane Cloud Forests*, Ecological Studies vol. 110, Springer-Verlag, New York, N. Y., pp. 38-78.
- Camilo, V. J., Tobón, C., and Breshears, D. D. 2008. Fog interception by non-vascular epiphytes in tropical montane cloud forests: Dependencies on gauge type and meteorological conditions. *Hydrol. Proc.* 22: 2484-2492.
- Cao, T., Yu, J., Song, G.-Y., Chen, Y., Xiu, C.-C., and Liu, Y. 2005. Biodiversity and distribution patterns of bryophytes in Shanghai City, China. *International Bryological Symposium for Prof. Pan-Cheih Chen's Centennial Birthday*, Nanjing, China, 25-31 October 2005, 60 pp.
- Chang, S. C., Lai, I. L., and Wu, J. T. 2002. Estimation of fog deposition on epiphytic bryophytes in a subtropical montane forest ecosystem in northeastern Taiwan. *Atmos. Res.* 64: 159-167.
- Clark, K. L. 1994. The role of epiphytic bryophytes in the net accumulation and cycling of nitrogen in a tropical montane cloud forest. Ph.D. dissertation, University of Florida, Gainesville, Florida, 271 pp.
- Clark, K. L. and Nadkarni, N. M. 1992. The capture and cascading of inorganic nitrogen in the canopy of a Neotropical cloud forest in Monteverde, Costa Rica. *Selbyana* 13: 148.
- Clark, K. L., Nadkarni, N. M., and Gholz, H. L. 1998a. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica* 30: 12-23.
- Clark, K. L., Nadkarni, N. M., Schaefer, D., and Gholz, H. L. 1998b. Atmospheric deposition and net retention of ions by the canopy in a tropical montane forest, Monteverde, Costa Rica. *J. Trop. Ecol.* 14: 27-45.
- Clark, D. L., Nadkarni, N. M., and Gholz, H. L. 2005. Retention of inorganic nitrogen by epiphytic bryophytes in a montane tropical forest. *Biotropica* 37: 328-336.
- Coxson, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Can. J. Bot.* 69: 2122-2129.
- Coxson, D. S., McIntyre, D. D., and Vogel, H. J. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). *Biotropica* 24(2a): 121-133.
- Dunne, H. J. F. van and Kappelle, M. 1998. Biomass diversity relations of epiphytic bryophytes on small *Quercus copeyensis* stems in a Costa Rican montane cloud forest. *Rev. Biol. Trop.* 46: 217-224.
- Edwards, P. J. and Grubb, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. *J. Ecol.* 65: 943-969.
- Fleischbein, K., Goller, R., Valarezo, C., Wilcke, W., Zech, W., and Knoblich, K. 2002. Die Rolle der Epiphyten und des LAI für die Interzeption in einem Bergregenwald der ecuadorianischen Anden. [The role of epiphytes and LAI for interception in a mountain rainforest of the Ecuadorian Andes.]. (Abstract). *Gesellschaft für Tropenökologie* 15: 98.
- Ford, L. 1994. The role of epiphytes in interception and retention of precipitation in rainforests. *Australasian Bryol. Newslett.* 31: 5.
- Frahm, J.-P. 1987. Which factors control the growth of epiphytic bryophytes in tropical rainforests? *Symp. Biol. Hung.* 35: 639-648.
- Frahm, J.-P. 1990a. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedw.* 51: 151-164.
- Frahm, J.-P. 1990b. Bryophyte phytomass in tropical ecosystems. *Bot. J. Linnean Soc.* 104: 22-33.
- Frahm, J.-P. 2003a. Climatic habitat differences of epiphytic lichens and bryophytes. *Cryptog. Bryol.* 24: 3-14.

- Frahm, J.-P. 2003b. Manual of Tropical Bryology. *Trop. Bryol.* 23: 1-196.
- Frahm, J.-P. and Kürschner, H. 1989. Was Moose auf die Bäume treibt. [What drives mosses on the trees.]. *Forschung* 4: 18-22.
- Franco, M. 1986. The influence of neighbours on the growth of modular organisms with an example from trees. *Phil. Trans. R. Soc. Lond. B* 313: 209-225.
- Frey, W., Goßow, R., and Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserleitenden und wasserspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (NordBorneo). [Distribution patterns of life forms, water-leaching and water-storing structures in epiphytic moss communities on Mt. Kinabalu (North Borneo).]. *Nova Hedw.* 51: 87-119.
- Gehrig-Downie, C., Obregón, A., Bendix, J., and Gradstein, S. R. 2013. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *J. Bryol.* 35: 243-254.
- Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. *Cryptog. Bryol.* 27(1): 141-152.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies.* Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R., Bock, C., Mandl, N., Nöske, N. M. 2007. Checklist Reserva Biológica San Francisco (Prov. Zamora-Chinchipe, S. Ecuador). *Ecotrop. Monogr.* 4: 69-87.
- Gradstein, S. R., Obregón, A., Gehrig, C., and Bendix, J. 2010. The tropical lowland cloud forest – a neglected forest type. In: Bruijnzeel, L. A., Scatena, F. N., and Hamilton, L. S. (eds.). *The Tropical Montane Cloud Forest.* Cambridge University Press, Cambridge, pp. 130-133.
- Greenwood, J. L. and Stark, L. R. 2014. The rate of drying determines the extent of desiccation tolerance in *Physcomitrella patens*. *Funct. Plant Biol.* 41: 460-467.
- Grieve, I. C., Proctor, J., and Cousins, S. A. 1990. Soil variation with altitude on Volcan Barva, Costa Rica. *Catena* 17: 525-534.
- Hattori, S. 1966 [1967]. Studies on the epiphytic moss flora of Japan 17. The epiphytic bryophyte communities in the coniferous forest of Mt. Honokawa, Shikoku. *J. Hattori Bot. Lab.* 29: 223-237.
- Hattori, S. and Iwatsuki, Z. 1970. The epiphytic bryophyte communities in the broad-leaved evergreen forests in the Tsushima Islands, Kyushu. Studies on the epiphytic moss flora of Japan, 19. *Mem. Natl. Sci. Mus. (Tokyo)* 3: 365-374.
- Hattori, S. and Kanno, S. 1956. The epiphytic moss community of the Kukuzo islet in southern Kyushu. *J. Jap. Bot.* 31: 42-46.
- Hattori, S. and Noguchi, A. 1954. On the bryophyte community of an *Abies firma* bole. *J. Hattori Bot. Lab.* 11: 93-98.
- Hattori, S., Iwatsuki, Z., and Kanno, S. 1956. Studies on the epiphytic moss flora of Japan. 3. The bryophytic community on *Ilex buergeri* in a hardwood forest side of mountain rivulet at Inohae in southern Kyushu. *J. Hattori Bot. Lab.* 16: 90-96.
- Herwitz, S. R. 1991. Aboveground adventitious roots and stemflow chemistry of *Ceratopetalum virchowii* in an Australian montane tropical rain forest. *Biotropica* 23: 210-218.
- Hietz, P., Wanek, W., Wania, R., and Nadkarni, N. M. 2002. Nitrogen-15 natural abundance in a montane cloud forest canopy as an indicator of nitrogen cycling and epiphyte nutrition. *Oecologia* 131: 350-355.
- Hofstede, R. G. M., Wolf, J. H. D., and Benzig, D. H. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forests. *Selbyana* 14: 37-45.
- Hofstede, R. G. M., Dickinson, K. J. M., and Mark, A. F. 2001. Distribution, abundance and biomass of epiphyte-lianoid communities in a New Zealand lowland *Nothofagus-podocarp* temperate rain forest: Tropical comparisons. *J. Biogeogr.* 28: 1033-1049.
- Hölscher, D., Köhler, L., Leuschner, C., and Kappelle, M. 2003. Nutrient fluxes in stemflow and throughfall in three successional stages of an upper montane rain forest in Costa Rica. *J. Trop. Ecol.* 19: 557-565.
- Hölscher, D., Köhler, L., Dijk, A. van, and Bruijnzeel, L. A. 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *J. Hydrol.* 292: 308-322.
- Holwerda, F., Bruijnzeel, L. A., Muñoz-Villers, L. E., Equihua, M., and Asbjornsen, H. 2010. Rainfall and cloud water interception in mature and secondary lower montane cloud forests of central Veracruz, Mexico. *J. Hydrol.* 384: 84-96.
- Horikawa, Y. 1932. Die epiphyllen Lebermoose von Japan. *Bot. Mag. (Tokyo)* 46: 176-187.
- Horikawa, Y. 1939. Three species of epiphyllous Hepaticae newly added to the Yakusima-flora. *J. Jap. Bot.* 15: 396-397.
- Horikawa, Y. 1948. Extension of the range of sword moss (*Bryoxiphium*) and epiphyllous Hepaticae of Japan. *Bot. Mag. (Tokyo)* 61: 81.
- Horikawa, Y. 1950. Some observations of the epiphytic bryophytes. *Hikobia* 1: 1-6.
- Horikawa, Y. and Nakanishi, S. 1954. On the growth-form types of epiphytic bryophytes. *Bull. Soc. Plant Ecol.* 3(4): 203-210.
- Hosokawa, T. 1950. Epiphyte-quotient. *Bot. Mag. (Tokyo)* 63(739-740): 18-21.
- Hosokawa, T. 1951. On the nomenclature of aerosynysis. *Bot. Mag. (Tokyo)* 64: 107-111.
- Hosokawa, T. 1953. On the nomenclature of Aerosynysiae. *Proc Seventh Internat. Bot. Cong. Stockholm 1950*, pp. 691-694.
- Hosokawa, T. 1954. On the *Campnosperma* forests of Kusaie in Micronesia, with special reference to the community units of epiphytes. *Vegetatio* 5: 351-360.
- Hosokawa, T. and Kubota, H. 1957. On the osmotic pressure and resistance to desiccation of epiphytic mosses from a beech forest, south-west Japan. *J. Ecol.* 45: 579-591.
- Hosokawa, T. and Odani, N. 1957. The daily compensation period and vertical ranges of epiphytes in a beech forest. *J. Ecol.* 45: 901-915.
- Hosokawa, T. and Omura, M. 1959. On a brief study of community dynamics of epiphytes. *Mem. Fac. Sci. Kyushu Univ. Ser. E (Biol.)* 3(1): 43-50.
- Hosokawa, T., Omura, M., and Nishihara, Y. 1954. Social units of epiphytic communities in forests. *Comm. 8e Congr. Internat. Bot., Paris, sect. 7*: 11-16.
- Hosokawa, T., Omura, M., and Nishihara, Y. 1957. Grading and integration of epiphytic communities. *Jap. J. Ecol.* 7: 93-98.
- Hosokawa, T., Odani, N., and Tagawa, H. 1964. Causality of the distribution of corticolous species in forests with special reference to the physio-ecological approach. *Bryologist* 67: 396-411.

- Hsu, C.-C., Horng, F.-W., and Kuo, C.-M. 2002. Epiphyte biomass and nutrient capital of a moist subtropical forest in north-eastern Taiwan. *J. Trop. Ecol.* 18: 659-670.
- Ingram, S. W. and Nadkarni, N. M. 1993. Composition and distribution of epiphytic organic matter in a Neotropical cloud forest, Costa Rica. *Biotropica* 25: 370-383.
- Iwatsuki, Z. 1960. The epiphytic bryophyte communities in Japan. *J. Hattori Bot. Lab.* 22: 160-352.
- Iwatsuki, Z. 1961. Notes on the epiphytic bryophyte communities in Japan, 1. *Misc. Bryol. Lichenol.* 2: 98-99.
- Iwatsuki, Z. 1962. Notes on the epiphytic bryophyte communities in Japan, 2. *Misc. Bryol. Lichenol.* 2: 100-102.
- Iwatsuki, Z. 1963a. *Andreaea rupestris* var. *fauriei* on bark. *J. Jap. Bot.* 38: 112.
- Iwatsuki, Z. 1963b. Notes on some Japanese species of the genus *Ulota*. *Misc. Bryol. Lichenol.* 3(3): 39.
- Iwatsuki, Z. and Hattori, S. 1955. Studies of the epiphytic moss flora of Japan. 1. The moss community on *Meliosma rigida* along a mountain stream. *J. Hattori Bot. Lab.* 15: 105-113.
- Iwatsuki, Z. and Hattori, S. 1956a. Studies on the epiphytic moss flora of Japan. 2. The bryophytic community on *Machilus japonica* in a dense hardwood forest in a valley at Inohae in southern Kyushu. *J. Hattori Bot. Lab.* 16: 83-90.
- Iwatsuki, Z. and Hattori, S. 1956b. Studies on the epiphytic moss flora of Japan. 3. The bryophytic community on *Ilex buergeri* in a hardwood forest side of a mountain rivulet at Inohae in southern Kyushu. *J. Hattori Bot. Lab.* 16: 90-96.
- Iwatsuki, Z. and Hattori, S. 1956c. Studies on the epiphytic moss flora of Japan. 4. The bryophytic community on *Cyclobalanopsis gilva* standing isolated on the margin of a hardwood forest in an open valley at Inohae in southern Kyushu. *J. Hattori Bot. Lab.* 16: 96-102.
- Iwatsuki, Z. and Hattori, S. 1956d. Studies on the epiphytic moss flora of Japan. 5. The bryophytic community on *Cinnamomum japonicum* in a hardwood forest on the mountain slope facing the west, at Wari'iwa in southern Kyushu. *J. Hattori Bot. Lab.* 16: 102-106.
- Iwatsuki, Z. and Hattori, S. 1956e. Studies on the epiphytic moss flora of Japan. 6. The bryophytic community on *Abies firma* and *Tsuga sieboldii* standing on a mountain slope at Wari'iwa in southern Kyushu. *J. Hattori Bot. Lab.* 16: 106-116.
- Iwatsuki, Z. and Hattori, S. 1956f. Studies on the epiphytic moss flora of Japan. 7. The bryophytic community on a large tree of *Cryptomeria japonica*, on the west slope of Mt. Ichifusa in southern Kyushu. *J. Hattori Bot. Lab.* 16: 116-121.
- Iwatsuki, Z. and Hattori, S. 1957. Epiphytic bryophyte communities on *Pinus pumila*, an alpine shrubby pine, in the Japanese Alps. *J. Jap. Bot.* 32: 125-127.
- Iwatsuki, Z. and Hattori, S. 1959a. Studies on the epiphytic moss flora of Japan. 10. The epiphytic bryophyte communities in the *Chamaecyparis obtusa* forest and the adjacent deciduous forest at Agematsu, central Japan. *J. Hattori Bot. Lab.* 21: 157-187.
- Iwatsuki, Z. and Hattori, S. 1959b. Studies on the epiphytic moss flora of Japan. 11. The epiphytic bryophyte communities in the beech forest in Shishibamiwari National Forest, central Japan. *J. Hattori Bot. Lab.* 21: 188-203.
- Iwatsuki, Z. and Hattori, S. 1965a. Studies on the epiphytic moss flora of Japan. 15. The epiphytic bryophyte communities in forests of the southernmost part of Akaishi Mountains, central Japan. *J. Hattori Bot. Lab.* 28: 221-232.
- Iwatsuki, Z. and Hattori, S. 1965b. Studies on the epiphytic moss flora of Japan. 16. The epiphytic bryophyte communities in a beech forest of Okinoyama National Forest, western Japan. *J. Hattori Bot. Lab.* 28: 233-238.
- Iwatsuki, Z. and Hattori, S. 1966. Studies on the epiphytic moss flora of Japan. 17. The epiphytic bryophyte communities in the coniferous forest of Mt. Honokawa, Shikoku. *J. Hattori Bot. Lab.* 29: 223-237.
- Iwatsuki, Z. and Hattori, S. 1968. Studies on the epiphytic moss flora of Japan. 18. The epiphytic bryophyte communities in the broad-leaved evergreen forests of Hanaze, southern Kyushu. *J. Hattori Bot. Lab.* 31: 189-197.
- Iwatsuki, Z. and Hattori, S. 1970. The epiphytic bryophyte communities in the broad-leaved evergreen forests in the Tsushima Islands, Kyushu. Studies on the epiphytic moss flora of Japan, 19. *Mem. Natl. Sci. Mus. (Tokyo)* 3: 365-374.
- Iwatsuki, Z. and Hattori, S. 1987. Microclimate at Inotani Valley near Nichinan, S. Japan. *Symp. Biol. Hung.* 35: 11-25.
- Jacobsen, N. H. G. 1978. An investigation into the ecology and productivity of epiphytic mosses. *J. S. Afr. Bot.* 44: 297-312.
- Johnson, A., and Kokila, P. 1970. The resistance to desiccation of ten species of tropical mosses. *Bryologist* 73: 682-686.
- Jordan, C. F., Golley, F. B., Hall, J. D., and Hall, J. 1980. Nutrient scavenging of rainfall by the canopy of an Amazonian rain forest. *Biotropica* 12: 61-66.
- Kamimura, M. 1939. Studies on the epiphyllous Hepaticae and its attached plants in Sikoku, Japan. *J. Jap. Bot.* 15: 62-83.
- Kao, W. Y., Chiu, Y. S., and Chen, W. H. 2000. Vertical profiles of CO₂ concentration and $\delta^{13}\text{C}$ values in a subalpine forest of Taiwan. *Bot. Bull. Acad. Sinica* 41: 213-218.
- Karger, D. N., Kluge, J., Abrahamczyk, S., Salazar, L., Homeier, J., Lehnert, M., Amoroso, V. B., and Kessler, M. 2012. Bryophyte cover of trees as proxy for air humidity in the tropics. *Ecol. Indic.* 20: 277-281.
- Klinge, H. 1963. Über Epiphytenhumus aus El Salvador, Zentralamerika. [About epiphyte humus from El Salvador, Central America.]. *Pedobiologia* 2: 102-108.
- Köhler, L. 2002. Die Bedeutung der Epiphyten im ökosystemaren Wasser- und Nährstoffumsatz verschiedener Altersstadien eines Bergregenwaldes in Costa Rica. [The importance of epiphytes in the ecosystem water and nutrient metabolism of different age stages of a mountain rainforest in Costa Rica.]. Ph.D. Dissertation. Berichte des Forschungszentrums Waldökosysteme Reihe A Bd. 181. University of Göttingen, Göttingen, 134 pp. + 12 pp. appendices.
- Köhler, L., Tobón, C., Frumau, K. A., and Bruijnzeel, L. S. 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecol.* 193: 171-184.
- Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserleitenden und wasserspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord-Borneo). *Nova Hedw.* 51: 87-119.
- Kürschner, H. 1995a. Epiphytische Moosengesellschaften im östlichen Kongobecken und den angrenzenden Gebirgsstöcken (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). Wissenschaftliche Ergebnisse der BRYOTROP – Expedition nach Zaire und Rwanda 4. [Epiphytic moss associations in the Eastern Congo basin and the adjoining highlands (National Park Kahuzi-Biega/Zaire, Nyungwe Forest/ Rwanda): Scientific results of the BRYOTROP-expedition to Zaire and Rwanda. No. 4.]. *Nova Hedw.* 61: 1-64.

- Kürschner, H. 1995b. Wissenschaftliche Ergebnisse der BRYOTROP-Expedition nach Zaire und Rwanda. 5. Höhengliederung epiphytischer Moose im Östlichen Kongobecken und den angrenzenden Gebirgsketten (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). [Scientific results of the BRYOTROP expedition to Zaire and Rwanda. 5. Elevation of epiphytic mosses in the Eastern Congo Basin and the adjacent mountain ranges (National Park of Kahuzi-Biega / Zaire, Forêt de Nyungwe / Rwanda).]. *Trop. Bryol.* 11: 77-86.
- Kürschner, H. 2003. Epiphytic bryophyte communities of southwestern Arabia – phytosociology, ecology and life strategies. *Nova Hedw.* 77: 55-71.
- Kürschner, H. 2004. Phytosociology, ecology and life strategies of a remarkable epiphytic bryophyte community of Socotra Island, Yemen. *Bot. Jahrb. Syst.* 125: 377-395.
- Kürschner, H. and Frey, W. 2013. Life strategies in bryophytes – a prime example for the evolution of functional types. *Nova Hedw.* 96: 83-116.
- Kürschner, H. and Parolly, G. 1998a. Syntaxonomy of trunk-epiphytic bryophyte communities of tropical rain forests: A first pantropical approach. *Phytocoenologia* 28: 357-425.
- Kürschner, H. and Parolly, G. 1998b. Lebensformen und Adaptationen zur Wasserleitung und Wasserspeicherung in epiphytischen Moosgesellschaften Nord-Perus (Amazonas-Tiefeland, Cordillera Oriental, Cordillera central). [Life forms and adaptations to water conduction and water storing in epiphytic bryophyte communities in northern Peru (the Amazon lowlands, eastern and central cordillera).]. *Nova Hedw.* 67: 349-379.
- Kürschner, H. and Parolly, G. 1999. Pantropical epiphytic rain forest bryophyte communities – Coeno-syntaxonomy and floristic-historical implications. *Phytocoenologia* 29: 1-52.
- Kürschner, H. and Parolly, G. 2004. Phytomass and water-storing capacity of epiphytic rain forest bryophyte communities in S Ecuador. Ecosociological studies in Ecuadorian bryophyte communities. IV. *Bot. Jahrb. Syst. Pflanz. Pflanz.* 125: 489-504.
- Lakatos, M., Obregón, A., Büdel, B., and Bendix, J. 2012. Midday dew – an overlooked factor enhancing photosynthetic activity of corticolous epiphytes in a wet tropical rain forest. *New Phytol.* 2012: 1-9.
- Laman, T. G. 1995. *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. *Ecology* 76: 2617-2626.
- Lawton, R. and Dryer, V. 1980. The vegetation of the Monteverde Cloud Forest Reserve. *Brenesia* 18: 101-116.
- Leary, J. J., Singleton, P. W., and Borthakur, D. 2004. Canopy nodulation of the endemic tree legume *Acacia koa* in the mesic forests of Hawaii. *Ecology* 85: 3151-3157.
- Lee, G. E. and Pócs, T. 2018. Additions to the distribution of some Palaeotropical *Lejeunea* (Marchantiophyta) species, with the description of *Lejeunea konratii* sp. nov. from Fiji. *Phytotaxa* 349: 31-38.
- León-Vargas, Y. 2001. Diversity of Epiphytic Bryophytes in a Montane Cloud Forest in the Venezuelan Andes. Ph.D. Diss. Univ. Bonn.
- León-Vargas, Y., Engwald, S., and Proctor, M. C. 2006. Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. *J. Biogeogr.* 33: 901-913.
- Liu, W., Fox, J. E. D., and Xu, Z. 2002. Nutrient fluxes in bulk precipitation, throughfall and stemflow in montane subtropical moist forest on Ailao Mountains in Yunnan, south-west China. *J. Trop. Ecol.* 18: 527-548.
- Löbs, N., Walter, D., Barbosa, C. G. G., Brill, S., Cerqueira, G. R., Sá, M. O., Araújo, A. C., Oliveira, L. R., Ditas, F., Moran-Zuloaga, D., Florentino, A. P. P., Wolff, S., Godoi, R. H. M., Kesselmeier, J., Oliveira, S. M., Andreae, M. O., Pöhlker, C., and Weber, B. 2019. Microclimatic and ecophysiological conditions experienced by epiphytic bryophytes in an Amazonian rain forest. *Biogeosciences* (in review).
- Lösch, R., Mülders, P., and Fischer, E. 1994. Scientific results of the BRYOTROP expedition to Zaire and Rwanda. 3. Photosynthetic gas exchange of bryophytes from different forest types in eastern Central Africa. *Trop. Bryol.* 9: 169-185.
- Matelson, T. J., Nadkarni, N. M., and Longino, J. T. 1993. Longevity of fallen epiphytes in a Neotropical montane forest. *Ecology* 74: 265-269.
- Matzek, V. and Vitousek, P. 2002. Nitrogen fixation in bryophytes, lichens, and dead wood along a soil-age gradient in Hawaii. Abstracts of the 87th Annual Meeting of the Ecological Society of America and the 14th Annual International Conference of the Society for Ecological Restoration, August 4-9, 2002, Tucson, AZ.
- Matzek, V. and Vitousek, P. 2003. Nitrogen fixation in bryophytes, lichens, and decaying wood along a soil-age gradient in Hawaiian montane rain forest. *Biotropica* 35(1): 12-19.
- Mizutani, M. 1966. Epiphyllous species of Lejeuneaceae from Sabah (North Borneo). *J. Hattori Bot. Lab.* 29: 153-170.
- Müller, U. G. and Frahm, J.-P. 1998. Diversität epiphytischer Moose eines westandinen Bergregenwaldes in Ecuador. [Diversity of epiphytic mosses of a Westand mountain rainforest in Ecuador.]. *Trop. Bryol.* 15: 29-44.
- Nadkarni, N. M. 1981. Canopy roots: Convergent evolution in rainforest nutrient cycles. *Science* 214: 1023-1024.
- Nadkarni, N. M. 1983. The Effects of Epiphytes on Nutrient Cycles within Temperate and Tropical Rainforest Tree Canopies. Ph. D. dissertation, University of Washington, Seattle.
- Nadkarni, N. M. 1984. Epiphyte biomass and nutrient capital of a Neotropical elfin forest. *Biotropica* 16: 249-256.
- Nadkarni, N. M. 1986. The effects of epiphytes on precipitation chemistry in a Neotropical cloud forest. *Selbyana* 9: 44-51.
- Nadkarni, N. M. 1994a. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Amer. Zool.* 34: 70-78.
- Nadkarni, N. M. 1994b. Factors affecting the initiation and elongation of above-ground adventitious roots in a tropical cloud forest tree: An experimental approach. *Oecologia* 100: 94-97.
- Nadkarni, N. M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica* 32: 358-363.
- Nadkarni, N. M. and Matelson, T. 1992. Biomass and nutrient dynamics of epiphyte litterfall in a Neotropical montane forest, Costa Rica. *Biotropica* 24: 24-30.
- Nadkarni, N. M. and Primack, R. B. 1989. A comparison of mineral uptake and translocation by above-ground and below-ground root systems of *Salix syringiana*. *Plant Soil* 113: 39-45.
- Nadkarni, N. M., Schaefer, D. A., Matelson, T. J., and Solano, R. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecol. Mgmt.* 198: 223-236.

- Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. *Bot. J. Linn. Soc.* 104: 281-291.
- Obregón, A., Gehrig-Downie, C., Gradstein, S. R., Rollenbeck, R., and Bendix, J. 2011. Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity. *Agric. Forest Meteorol.* 151: 290-300.
- Oliveira, S. M. 2018. The double role of pigmentation and convolute leaves in community assemblage of Amazonian epiphytic Lejeuneaceae. *PeerJ* 6:e5921 <<http://doi.org/10.7717/peerj.5921>>.
- Oliveira, S. M., Steege, H. ter, Cornelissen, J. H., and Gradstein, S. R. 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: A regional approach. *J. Biogeogr.* 36: 2076-2084.
- Pardow, A. and Lakatos, M. 2012. Desiccation tolerance and global change: Implications for tropical bryophytes in lowland forests. *Biotropica* 45: 27-36.
- Pardow, A., Gehrig-Downie, C., Gradstein, R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. *Biodiv. Conserv.* 21: 3637-3655.
- Parolly, G. and Kürschner, H. 2004. Ecosociological studies in Ecuadorian bryophyte communities I. Syntaxonomy, life strategies and ecomorphology of the oreale epiphytic vegetation of S. Ecuador. *Nova Hedw.* 78: 1-43.
- Pentecost, A. 1998. Some observations on the biomass and distribution of cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains, Uganda. *Global Ecol. Biogeogr. Lett.* 7: 273-284.
- Peterson, G., Moyá, M. T., Zotz, G., Goslin, M., Kay, A., Maple, M., and Reich, A. 1994. Estimation of water loss rates in epiphytes. *Trop. Biol.: Ecol. Appr.* 94: 35-37.
- Pócs, T. 1976. The role of epiphytic vegetation in the water balance and humus production of the rainforests of the Uluguru Mountains, East Africa. *Bossiera* 24: 499-503.
- Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Acad. Sci. Hung.* 26: 143-167.
- Pócs, T. 1989. 28. A preliminary study of the undergrowth of primary and secondary submontane rainforests in the East Usambara Mountains, with notes on epiphytes. In: Hamilton, A. C. and Bensted-Smith, R. (eds.). *Forest Conservation in the East Usambaras*. IUCN – The World Conservation Union Forest Division, Ministry of Lands, Natural Resources and Tourism United Republic of Tanzania, pp. 301-306.
- Proctor, M. C. F. 2002. Ecophysiological measurements on two pendulous forest mosses from Uganda, *Pilotrichella ampullacea* and *Floribundaria floribunda*. *J. Bryol.* 24: 223-232.
- Prosperi, J. and Michaloud, G. 2001. Epiphytes and their contribution to canopy diversity. *Plant Ecol.* 153: 51-63.
- Reenen, G. B. A. van and Gradstein, S. R. 1983. Studies on Colombian cryptogams. XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Bot. Neerl.* 32: 163-175.
- Renner, O. 1932. Zur Kenntnis des Wasserhaushaltes javanischer Kleinepiphyten. Mit einem Anhang: Zu den osmotischen Zustandsgrößen. [For the knowledge of the water balance of Javanese small epiphytes. With an appendix: To the osmotic state variables.]. *Planta* 18: 215-287.
- Rhoades, F. M. 1995. Nonvascular epiphytes in forest canopies: Worldwide distribution, abundance, and ecological roles. In: Lowman, M. and Nadkarni, N. (eds.). *Forest Canopies*. Academic Press, New York, pp. 353-408.
- Richards, P. W. 1984. Introduction. In: Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*. Academic Press, New York, pp. 1-8.
- Romero, C., Putz, F. E., and Kitajima, K. 2006. Ecophysiology in relation to exposure of pendant epiphytic bryophytes in the canopy of a tropical montane oak forest. *Biotropica* 38: 35-41.
- Sanford, R. L. Jr. 1987. Apogeotropic roots in an Amazon rain forest. *Science* 235: 1062-1064.
- Santon, D. E. and Horn H. S. 2013. Epiphytes as "filter-drinkers": Life-form changes across a fog gradient. *Bryologist* 116: 34-42.
- Silva, M. P. P. and Pôrto, K. C. 2013. Bryophyte communities along horizontal and vertical gradients in a human-modified Atlantic Forest remnant. *Botany* 91: 155-166.
- Sporn, S. G. 2009. Epiphytic bryophytes in natural forests and cacao agroforests of Central Sulawesi, Indonesia. Ph.D. dissertation, Georg-August-Universität Göttingen, 129 pp.
- Sporn, S. G., Bos, M. M., Hoffstätter-Müncheberg, M., Kessler, M., and Gradstein, S. R. 2009. Microclimate determines community composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforests in Indonesia. *Funct. Plant Biol.* 36: 171-179.
- Stuntz, S., Simon, U., and Zotz, G. 2002. Rain forest air-conditioning: The moderating influence of epiphytes on the microclimate in tropical tree crowns. *Internat. J. Biometeorol.* 46: 53-59.
- Thompson, S. L., Yates, D. J., and Bergstrom, D. M. 1994. Water-holding capacity of epiphytic bryophytes in subtropical forests. *Austral. Bryol. News.* 31: 6.
- Tixier, P. 1966. Flore et Végétation Orophiles de l'Ase Tropicale: Les Epiphytes du flanc méridional du Massif Sud Annamitique. [Orophile flora and vegetation of the Tropical Ase: The epiphytes of the southern flank of the Annamitic South Massif.]. Ph.D. dissertation, Paris.
- Vance, E. D. and Nadkarni, N. M. 1990. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. *Soil Biol. Biochem.* 22: 677-684.
- Vance, E. D. and Nadkarni, N. M. 1992. Root biomass distribution in a moist tropical montane forest. *Plant Soil* 142: 31-39.
- Veneklaas, E. J. 1990. Nutrient fluxes in bulk precipitation and throughfall in two montane tropical rain forests, Colombia. *J. Ecol.* 78: 974-992.
- Veneklaas, E. J. and Ek, R. van. 1990. Rainfall interception in two tropical montane rain forests, Colombia. *Hydrol. Process.* 4: 311-326.
- Veneklaas, E. J., Zagt, R. J., Leerdam, A. van, Ek, R. van, Broekhoven, A. J., and Genderen, M. van. 1990. Hydrological properties of the epiphytic biomass of a montane tropical rainforest, Colombia. *Vegetatio* 89: 183-192.
- Vitousek, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- Wagner, S., Zotz, G., and Bader, M. Y. 2013. The temperature acclimation potential of tropical bryophytes. *Plant Biol.* 29: 277-290.
- Waite, M. and Sack, L. 2010. How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10

- Hawaiian species of contrasting light habitats. *New Phytol.* 185: 156-172.
- Wanek, W. and Pörtl, K. 2008. Short-term ^{15}N uptake kinetics and nitrogen nutrition of bryophytes in a lowland rainforest, Costa Rica. *Funct. Plant Biol.* 35: 51-62.
- Wania, R., Hietz, P., and Wanek, W. 2002. Natural ^{15}N abundance of epiphytes depends on the position within the forest canopy: Source signals and isotope fractionation. *Plant Cell Environ.* 25: 581-589.
- Went, F. W. 1940. Soziologie der epiphyten eines tropischen Urwaldes. [Sociology of the epiphytes of a tropical jungle.]. *Ann. Jard. Bot. Buitenzorg* 50: 1-98.
- Werner, F. A. and Gradstein, S. R. 2009. Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. *J. Veg. Sci.* 20: 59-68.
- Wilcke, W., Yasin, S., Valarezo, C., and Zech, W. 2001. Change in water quality during the passage through a tropical montane rain forest in Ecuador. *Biogeochemistry* 55: 45-72.
- Wolf, J. H. D. 1993a. Epiphyte communities of tropical montane rain forest in the northern Andes. I. Lower montane communities. *Phytocoenologia* 22: 1-52.
- Wolf, J. H. D. 1993b. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Missouri Bot. Gard.* 80: 928-960.
- Wolf, J. H. D. 1993c. Epiphyte communities of tropical montane rain forest in the northern Andes. II. Upper montane communities. *Phytocoenologia* 22: 53-103.
- Zotz, G., Büdel, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO_2 exchange of tropical bryophytes in a lower montane rainforest in Panama. *Bot. Acta* 110: 9-17.

CHAPTER 8-4

TROPICS: EPIPHYTE ECOLOGY, PART 2

TABLE OF CONTENTS

Adaptations	8-4-2
Growth Forms and Life Forms.....	8-4-2
Life Cycle Strategies.....	8-4-7
Dispersal and Colonization	8-4-8
Host Trees	8-4-12
Height on Tree	8-4-15
Tree Base	8-4-22
Upper Trunk.....	8-4-27
Lower Branches	8-4-28
Twigs	8-4-29
Canopy	8-4-30
Logs and Rotten Wood.....	8-4-31
Sampling	8-4-35
Quadrats	8-4-36
Rope Climbing.....	8-4-37
Bow and Arrow.....	8-4-38
Other Canopy Access.....	8-4-39
Role	8-4-40
Adventitious Roots.....	8-4-40
Substrata for Tracheophytes.....	8-4-41
Friend or Foe?	8-4-42
Faunal Habitat.....	8-4-42
Summary	8-4-43
Acknowledgments.....	8-4-43
Literature Cited	8-4-43

CHAPTER 8-4

TROPICS: EPIPHYTE ECOLOGY, PART 2



Figure 1. Mossy forest in rainy season on Reunion Island. Bryophytes surround the branches like a muff. Photo Courtesy of Min Chuah-Petiot.

Adaptations

Living on trees often puts the bryophytes at the mercy of rainfall (where there is no fog), either as throughfall or stemflow. Thus, special adaptations are necessary for those times when it is not raining, for the substrate is unlikely to do much to maintain the humidity (Frahm & Kürschner 1989). Gradstein and Pócs (1989) suggest a number of adaptations that permit these taxa to be so successful in this living habitat:

1. **Green, multicellular spores** with **endosporous** development (Figure 2) [e.g. **Dicnemonaceae** (Figure 3), **Lejeuneaceae** (Figure 5, Figure 7-Figure 8)] (Nehira 1983), permitting the protonema to get a quick start.
2. **Sexual dimorphism** and **phyllo dioicy** (having dwarf males that live on leaves or tomentum of females; Figure 4), possibly increasing gene flow by ensuring that males are close to females.
3. Numerous means of **asexual reproduction**, **monoicous** condition, and **neoteny** (sexual maturity at early developmental stage; Figure 5), permitting movement from place to place among **ephemeral** (short-lived) substrata [e.g. **Lejeuneaceae** (Figure 5, Figure 7-Figure 8)] (Schuster 1984; Richards 1984).
4. **Rhizoid discs** (Figure 6) for anchorage and adhesion (Winkler 1967).
5. **Lobules** [**Frullaniaceae** (Figure 67), **Lejeuneaceae** (Figure 5, Figure 7-Figure 8)] and **hyaline leaf margins** for absorption and retention of water; **Colura** (Figure 7-Figure 8) even has a closing apparatus at the entrance of its lobule (Jovet-Ast

1953). Many **Calymperaceae** (Figure 9) have **hyaline cells** (Figure 10) in their leaves (Richards 1984).

6. **Cushion** life form (Figure 25) on branches of open montane forests (Pócs 1982).

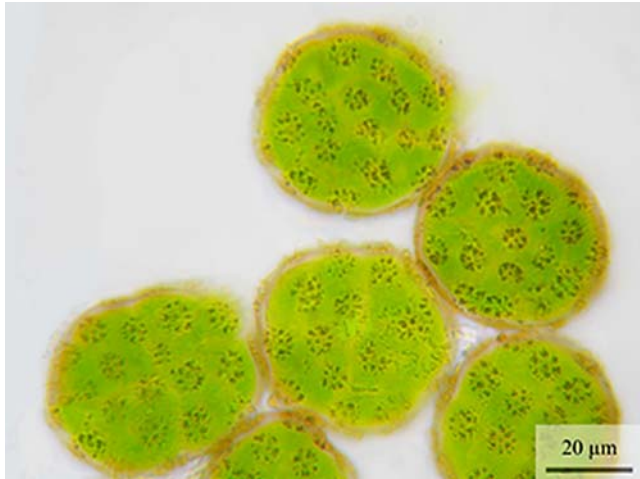


Figure 2. *Frullania ericoides* multicellular green endospores, demonstrating their germination within the spore. Photo modified from Silva-e-Costa *et al.* 2017, through Creative Commons.



Figure 3. *Dicnemon* sp., a genus with endosporic development. Photo by Vita Plášek, with permission.



Figure 4. *Leucobryum candidum* with dwarf males, showing **phylloidiocy**. Photo by Paddy Dalton, with permission.

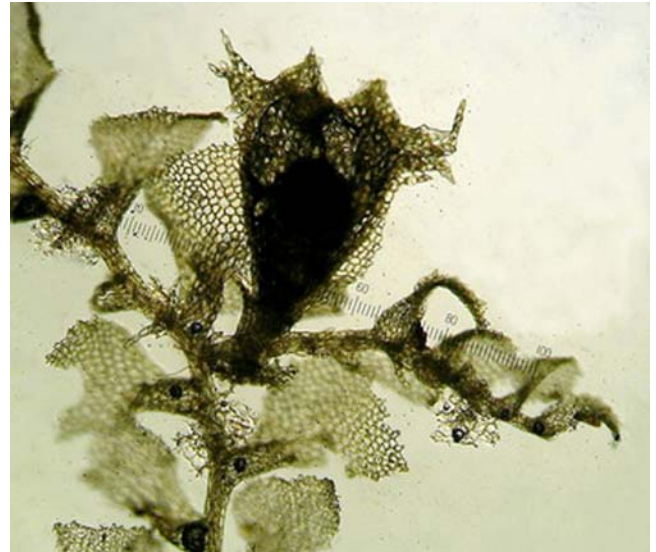


Figure 5. *Drepanolejeunea inchoata* with perianth, an example of **neoteny** in the **Lejeuneaceae**. Photo by Michaela Sonnleitner, with permission.



Figure 6. *Frullania* rhizoids. Photo courtesy of Andi Cairns.



Figure 7. *Colura calyptrifolia* on willow, with lobules showing. Photo by Stan Phillips, through public domain.

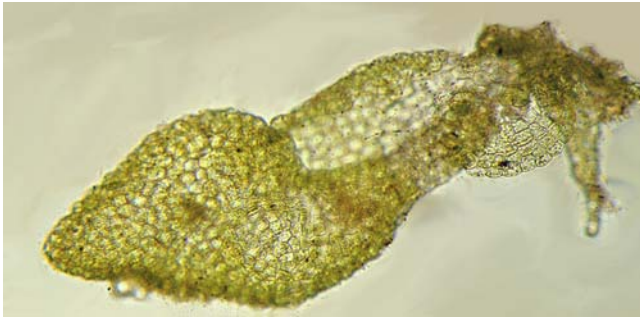


Figure 8. *Colura* leaf showing lobule. Photo courtesy of Jan-Peter Frahm.



Figure 9. *Leucophanes molleri* (Calymperaceae). Some members of this family have hyaline cells in their leaves. Photo courtesy of Noris Salazar Allen.



Figure 10. *Leucophanes molleri* (Calymperaceae) leaf cross section showing hyaline cells surrounding photosynthetic cells. Photo courtesy of Noris Salazar Allen.

Frey *et al.* (1990) studied the epiphytes in Mt. Kinabalu (Figure 11) in North Borneo. They examined distribution patterns of life forms and the water-storing structures in epiphytes. They also looked at their role in water leaching, an important aspect in tropical forest nutrient cycling. Other useful studies on adaptations include those of Thiers (1988 – **Jungermanniales**, *i.e.* leafy liverworts; Figure 5, Figure 7) and Kürschner (2000 – adaptations in the tropical rainforest).



Figure 11. Mt Kinabalu in Borneo. Photo through Creative Commons.

Growth Forms and Life Forms

Growth forms, life forms, and life cycle strategies interact with other adaptations to provide the bryophytes with the best strategy for a particular environment. The main reference for growth or life forms of bryophytes is Mägdefrau 1982 and for life strategies During 1979. See also Volume 1, Chapter 4, of this series on Bryophyte Ecology for details on these.

Based on a number of pilot studies in the tropics (Frahm 1990; Frey *et al.* 1990, 1995; Frey & Kürschner 1991; Kürschner & Seifert 1995; Kürschner & Parolly 1998b; Kürschner *et al.* 1998), Kürschner *et al.* (1999) described generalizations of tropical growth forms, life forms, and life strategies for the epiphyte habitat. **Perennial stayers** and **perennial shuttles** species (see During 1979) are important life cycle strategies in most of the tropics. They dominate in the tropical lowland and submontane belt as well as in the cooler and more humid montane rainforest. However, in the former two they are **mat formers**, whereas in the montane rainforest they are mostly **fans** and **wefts** that rely on propagules and clonal growth. Some species have ciliate leaves that are able to collect water from fog. In the more xeric conditions of the open, upper montane forests, **short turfs**, **tall turfs**, and **cushions** predominate, but are also **perennial stayers** and **perennial shuttles** species. **Colonists**, by contrast, occur almost exclusively in secondary forests. Kürschner and coworkers considered these relationships to apply throughout the tropics.

In the Sulawesi rainforest (Figure 12) in Indonesia, the understory has a preponderance of **dendroid** and **fan-like** species of bryophytes, whereas the crowns of the trees have more **tuft** species than other types (Sporn *et al.* 2010). Like many other factors, this reflects the differences in microclimate between the upper canopy and the understory,

but it also reflects differences in substrate provided by understory trees vs canopy trees.



Figure 12. Mountains of South Sulawesi, Indonesia. Photo by Achmad Rabin Taim, through Creative Commons.

Kürschner and Seifert (1995) described epiphytic communities in the eastern Congo basin (Figure 13) and nearby mountain ranges. These included consideration of life forms and water storage.



Figure 13. Forests in the Democratic Republic of the Congo. Photo from Bobulix, through Creative Commons.

Bryophyte life forms in flooded and non-flooded habitats in the Colombian Amazon (Figure 14-Figure 15) reflect the differences in humidity (Benavides *et al.* (2004). In the floodplains, the **fan** and **mat** forms predominate, whereas more epiphytic liverworts occur in the non-flooded forest.

Leerdam *et al.* (1990) described the epiphytes of a Colombian cloud forest (Figure 16). Bryophytes comprise most of the biomass. They found a sequence of life forms along the canopy branches, creating two groups: inner canopy and outer canopy. These are mostly **tall turfs** and **smooth mats**, respectively. The life forms corresponded with microclimatological factors, water and nutrient availability, and substratum age. The phorophyte species also influence the type of growth and life forms that grow there.



Figure 14. Amazon rainforest. Photo by Phil Harris, through Creative Commons.



Figure 15. Colombian Amazon. Photo by Actorsuarez, through Creative Commons.



Figure 16. Colombian cloud forest with White Yarumo. Photo by Alejandro Bayer Tamayo, through Creative Commons.

Some striking life forms that are almost exclusively tropical are the **feather**, **bracket**, and **pendent** (Figure 17) forms. These seem to reflect the high atmospheric humidity around the first few meters of the tree bole, where little air stirs to carry away the moisture quickly.

Pendent (Figure 17) bryophytes are common in areas with high humidity. Proctor (2004) examined the light and desiccation responses of two of these **pendent** taxa [*Weymouthia mollis* (Figure 18) and *W. cochlearifolia*

(Figure 19)]. *Weymouthia cochlearifolia* is more typical forming patches on the trunk and branches, but it can grow as a **pendent** form. *Weymouthia mollis* typically grows as a **pendent** form. *Weymouthia cochlearifolia* reached 95% saturation at $160 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, whereas *W. mollis* ranged $176\text{--}307 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD or even more. They demonstrated the primary needs of **pendent** forms: high levels and reasonably regular precipitation, shelter from wind, and moderate shade. From this they surmised that exposure and the high evaporation rate that accompanies it will favor **small cushions** or **smooth mat** life forms. Proctor reasoned that exposure would minimize the boundary-layer resistance to CO_2 uptake and maximize the mechanical effects of wind. **Tight cushions** and **smooth mats** can more easily resist these. On the other hand, the more open life forms are more exposed for efficient light interception and CO_2 uptake.



Figure 19. *Weymouthia cochlearifolia*, a species that can form both **mats** and **pendent** forms. Photo by Niels Klazenga, with permission.



Figure 17. *Cheilolejeunea jackii* **pendent** liverwort on the Galapagos Islands. Photo courtesy of Robbert Gradstein.



Figure 18. *Weymouthia mollis*, a species that is typically **pendent**, in Chile. Photo by Juan Larrain, with permission.

Some bryophyte species develop different life forms based on their habitat (Ford 1994). For example in Queensland *Papillaria* (Figure 20) spp. on *Sloanea woollsii* (Figure 22) exhibit forms ranging from **long pendent** forms in the canopy branches to **creeping mats** on lower branches and the upper trunk. **Dendroid** forms are especially common on tree trunks. Stumps have mosses such as the dominant *Camptochaete vaga* (see Figure 21), but also can have *Dicranum* spp. (see Figure 23)



Figure 20. *Papillaria crocea* in a cloud forest at Mt Budawang, Australia. Photo by Peter Woodard, through public domain.



Figure 21. *Camptochaete* sp. from New Zealand. Photo by Jan-Peter Frahm, with permission.



Figure 22. *Sloanea woollsii* with epiphytes on the base and trunk. Photo by Peter Woodard, through public domain.



Figure 23. *Dicranum* sp., a cushion former from the Neotropics. Photo by Michael Lüth, with permission.

Additional references on tropical bryophyte life forms include those of Kürschner and Parolly (1998a, 2005, 2007).

Life Cycle Strategies

One of the most important adaptations to tropical climates is that of life cycle strategies. These must be timed to coordinate with wet and dry periods. Sperm require at least some water for transfer. Spores are dispersed best by dry winds.

Furthermore, life strategies of epiphytic bryophytes change with altitude. Frey *et al.* (1995) compared these strategies in the eastern Congo basin (Figure 24), a tropical lowland. In the primary rainforests of the tropical lowland and lower montane, the epiphytes were generally **perennial shuttle** species and **perennial stayers**. These had low to moderate sexual and asexual reproduction. This strategy combination is well suited for the high temperature and humidity regime, particularly for the leafy liverworts that dominate these communities. In the montane rainforests and cloud forests the perennial shuttle species have high asexual reproduction, with both propagules and clonal growth contributing. In **secondary woodlands** (areas of regrowth), ericaceous woodlands, and subpáramo of African volcanoes, the perennial shuttle and perennial stayers with high levels of sexual reproduction reach their greatest numbers. This is facilitated by the regular production of sporophytes in the **xeric** (dry) conditions with a strong **diurnal** (daily) climate. This reproductive strategy is typical of epiphytes in xeric woodlands.



Figure 24. Lowland rainforest, Congo Basin, Cameroon. Photo by Mauri Rautkari, through Creative Commons.

Kürschner (2003) described the life strategies of two epiphytic bryophyte associations in southwestern Arabia. The species are mostly drought tolerant. Their life strategies are distinctly correlated with their ecological site conditions. The *Orthotricho* (Figure 25)-*Fabronietum socotranae* (Figure 26) is a drought-tolerant association dominated by **cushions**, **short turf**, and **mats** – **perennial stayers** with regular sporophyte formation. By contrast, in the sub-humid *Leptodonto* (Figure 27)-*Leucodontetum schweinfurthii* (Figure 28) association, the typical life forms are **tails** and **fans**. These are **pleurocarpous perennial shuttle** species that have large spores. These large spores limit them to short-range dispersal, relatively low reproductive rates, and generative reproduction. This association has a much higher diversity of life forms and life strategies, including liverworts.



Figure 25. *Orthotrichum tasmanicum* with capsules. Photo by David Tng, with permission.



Figure 26. *Fabronia pusilla*; in Arabia *Orthotricho-Fabronietum socotranæ* is a common association. Photo by Michael Lüth, with permission.



Figure 27. *Leptodon longisetus* from Tenerife; this genus forms the *Leptodonto-Leucodontetum schweinfurthii* association in humid Arabia. Photo by Jonathan Sleath, with permission.



Figure 28. *Leucodon julaceus*; this genus forms the *Leptodonto-Leucodontetum schweinfurthii* association in humid Arabia. Photo by Bob Klips, with permission.

Spore size is an adaptive trait wherein small spores have a good chance for long-distance dispersal and large spores do not, but have a greater chance for successful germination and establishment (Kürschner & Parolly 1998a). Few bryophytes are able to use both strategies. However, one notable exception is an epiphytic **heterosporous** (having two sizes of spores) moss of the Andes of northern Peru – *Leptodontium viticulosoides* (Figure 29).



Figure 29. *Leptodontium viticulosoides*, a heterosporous species that uses both long-distance dispersal of small spores and more successful establishment of large spores. Photo by Claudio Delgadillo Moya, with permission.

Having similar adaptive traits in similar conditions is common among bryophytic epiphytes (Kürschner 2003, 2004a) – a product of convergent evolution. This convergence is common among life strategies of tropical bryophytes.

Additional studies on life strategies include Egunyomi and Olarinmoye (1983), Kürschner (2004b), Kürschner and Parolly (2005, 2007), and Kürschner *et al.* (2006, 2007).

Dispersal and Colonization

Colonization must be preceded by dispersal. Thus, to examine colonization rates, we must necessarily understand the limitations to dispersal.

Yeaton and Gladstone (1982) examined colonization patterns of epiphytic orchids on calabash trees (*Crescentia alata*; Figure 30) in Costa Rica. They hypothesized that the

number of propagules produced by the species determined the colonization pattern. The same hypothesis can be considered for bryophytes.



Figure 30. *Crescentia alata* in Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Wolf (1994) examined the factors that control the distribution of bryophytes and lichens in the northern Andes (Figure 31). He concluded that randomness of propagule supply appears to be the most important factor in determining the epiphyte composition on branch and trunk segments.



Figure 31. Northern Andes in Colombia. Photo by Conocer, through public domain.

But Mari *et al.* (2016) reached a somewhat different conclusion. They avoided the differences among **phorophytes** (plants on which epiphytes grow) by sampling only one tree species, *Aldina heterophylla* (a legume). This is a dominant species in the Amazonian white-sand habitats and sports heavy loads of epiphytes. Mari and coworkers attempted to quantify the importance of the tree zone in colonization by comparing geographic distances at scales of 100 m² and 2,500 km². At the larger, regional scale, the tree zone explained approximately two-thirds of the primary compositional gradient – a factor more than double that accounted for by site differences. On the other hand, spatial effects were absent at the fine scale of 100 m², with more dissimilarity than expected by chance when compared to communities on neighboring

phorophytes. The researchers concluded that microsite availability, not dispersal limitation, is the most important factor in structuring the epiphytic communities of this forest type.

The **phorophyte** itself can play a role in the colonization (Olarinmoye 1977). Such factors as bark roughness and smoothness determine whether a propagule is able to adhere once it arrives. Leachates from the host leaves could inhibit growth, but for the leafy liverwort *Radula flaccida* (Figure 32), it was only extracts, not leachates, that inhibited growth (Olarinmoye 1981, 1982).



Figure 32. *Radula flaccida* habit with gemmae. Extracts, but not leachates, from tree leaves inhibited growth on the phorophyte host. Photo by Michaela Sonnleitner, with permission.

Oliveira *et al.* (2009) noted the gradient of bryophyte species communities from the base of the tree to the top of the canopy in the Guianas (Figure 33), highlighting the role of niche assembly in defining these communities. They set out to test whether niche assembly, rather than dispersal limitation, drives species composition of epiphytic bryophyte communities on a large spatial scale. Using three lowland forests, they sampled six different height zones of several trees in each. They tested whether specialists maintain a preferred height zone across the Guianas. They found that 57% of the species had a preferred height zone throughout the localities. In fact, the communities were more similar across 640 km at the same height zone than they were among the heights on any single tree. Hence, they concluded that niche assembly was a stronger determinant of the communities than were dispersal factors on both local and regional scales.



Figure 33. French Guiana tropical forest. Photo by Cayambe, through Creative Commons.

While the similarity within a zone is greater even at 640 km than among height zones of a tree, the similarity within the same locality is greater than that with greater distances (Oliveira & ter Steege 2015). Using nine localities across 2800 km from east to west in the Amazon forest (Figure 14), these researchers again demonstrated that height zone explains most of the variation among communities. The outer canopy communities exhibit the greatest similarity between trees and localities. The variation at the geographic scale could be explained primarily by elevation and temperature.

Oliveira and ter Steege (2015) furthermore found that establishment limitation is strongest at the extremes of the vertical gradient. Communities of the tree base and the outer canopy draw individuals from outside the habitat species pool at a rate of 0.28 and 0.22, respectively, in contrast with values between 0.55 and 0.76 of other height zones, contrasting with the hypothesis that species inhabiting the canopy have higher chances of engaging in long-distance dispersal events (see *e.g.* Gradstein 2006, p. 17). Whereas the canopy may have a greater exposure to propagules that are in the air currents, they are also subject to winds that can dislodge the propagules. They might also be limited by propagule availability as those propagules might be constrained by their canopy of origin, preventing them from entering the air currents. Oliveira and ter Steege suggested that bryophytes in these two extreme zones (outer canopy and tree base) might be, through time, subjected to stronger selection.

Hietz (1997) studied the population dynamics of epiphytes in a Mexican humid montane forest. He used repeated photographs to follow 5,124 individuals (44 species) for more than two years. This study demonstrated the importance of branch loss as a contributor to the mortality of epiphytic flowering plants and ferns.

Nadkarni (2000) performed one of the few experimental studies on colonization by epiphytes. She stripped branch surfaces of their epiphytes in a lower montane cloud forest, then tracked what landed where and whether it was able to remain where it landed. Epiphytes are lost from the canopy due to sloughing, branch breakage, and treefalls, typically caused by wind or heavy rainfall. Most of our understanding of colonization patterns has been from studying forests of a series of ages and comparing their floras. In the temperate forest, colonization is rapid, with up to 6 cm elongation in the first year. Furthermore, the composition is similar to that of the original community. But in the tropical forest, colonization is very slow, exhibiting no colonization in the first five years! The new colonization furthermore differs markedly from the original communities. Instead of the dead organic matter, bryophytes, and tracheophytes of the mature branch community, the new community begins with crustose and foliose lichens. Even more surprising is that instead of encroachment from the sides, the colonizers enter the bare areas from the bottom up. In the sixth year, algae and bryophytes begin to colonize the lower sides of branches. This appears to be related to the greater moisture on that side of the branch.

Nadkarni (2000) concluded that bare branches, typically with smooth bark, retain little moisture and are

unsuitable for the developing epiphytes. Once early lichens become established, more water is retained, permitting growth of species adapted to frequent drying. As colonization increases, nutrients as well as water are retained, permitting larger and less xerophytic species to survive. She further surmised that at the branch tips, where colonization is much more rapid, the small branches are more able to trap and hold propagules, and they are more exposed to fog and mist, thus having more available moisture. In both cases, once the bryophytes become established, the better retention of water and nutrients facilitates a more rapid continuation of the colonization.

In a separate study, Nadkarni *et al.* (2000) experimented with artificially dispersing bryophyte fragments in a tropical montane cloud forest of Costa Rica, using quadrats above branches of saplings and mature trees of *Ocotea tonduzii* (see Figure 34). Only 1% of the dispersed fragments were retained by the sapling crowns for the six months of the study. On the other hand, branches in the forest canopy, already possessing intact epiphyte communities, retained 24% of the dropped bryophytes. Branches that had been stripped of their epiphytes retained only 5%.



Figure 34. *Ocotea minarum*; *Ocotea tonduzii* was used to study adherence of bryophyte fragments in Costa Rica. Photo by Denise Sasaki, through Creative Commons.

Colonization of bryophytes can be important to establish a suitable habitat for larger epiphytes such as orchids. Zotz and Vollrath (2003) found that epiphytes on the palm *Socratea exorrhiza* (Figure 35-Figure 36) become established in bryophyte clumps (Figure 36) more often than could be expected from randomness, but they nevertheless do not seem to depend on them 100%. This enhancement of the habitat by bryophytes most likely accounts for the delay in tracheophyte colonization until the trees are at least 20 years old.



Figure 35. *Socratea exorrhiza* in Brazil. Photo by Andrew J. Henderson, Palmweb, through Creative Commons.



Figure 36. *Socratea exorrhiza* with various tracheophyte epiphytes established in bryophytic epiphytes. Photo by David J. Stang, through Creative Commons.

A number of ant species live in the trees in the tropics and some even build nests using tracheophytes (Longino & Nadkarni 1990; Blüthgen *et al.* 2001). In Costa Rica, these ants often make nests in arboreal litter, mosses, and humus that accumulate under the canopy epiphytic tracheophytes. The species in the canopy are rarely found on the ground and their travels among the canopy branches are likely to contribute to the dispersal of bryophyte fragments,

gemmae, and spores. Their role in dispersal needs to be explored quantitatively.

In contrast with the experimental colonization study by Nadkarni (2000), Frahm *et al.* (2000) observed that crustose lichens seemed to inhibit epiphytic bryophyte growth. They tested extracts of these lichens and bark samples on spore germination of the soil bryophytes *Ceratodon purpureus* (Figure 37) and *Funaria hygrometrica* (Figure 38). These extracts inhibit spore germination of these two species. They also tested the extracts on seeds of the bromeliad *Vriesea splendens* (Figure 39) and the soil-dwelling mustard *Lepidium sativum* (Figure 40). The extracts reduce the germination of seeds of *Vriesea*, but they actually promote germination of *Lepidium*. Thus we cannot conclude from this study of soil species whether the crustose lichens actually inhibit growth of bryophytes that are normally epiphytes, but the results suggest that such interaction needs to be tested.



Figure 37. *Ceratodon purpureus* with young sporophytes, a soil-dwelling species whose spore germination is inhibited by at least some lichen extracts. Photo by Hermann Schachner, through Creative Commons.



Figure 38. *Funaria hygrometrica* with young sporophytes, a soil-dwelling species whose spore germination is inhibited by some lichen extracts. Photo by Hermann Schachner, through Creative Commons.



Figure 39. *Vriesea splendens*; germination of seeds in this species are inhibited by lichen extracts. Photo by Bernard Dupont, through Creative Commons.



Figure 40. *Lepidium sativum*, a species in which seed germination is enhanced by lichen extracts. Photo by Dinesh Valke, through Creative Commons.

Barkman (1958) and Pócs (1980) suggested that bryophytes may cause their own displacement by retaining water that makes tracheophytic epiphyte presence possible. They furthermore form humus, accelerate bark decay (Barkman 1958), and facilitate anchorage of seeds and other propagules.

Host Trees

Specific bryophyte-host relationships have been reported a number of times in temperate regions where tree species richness is very low, as for example those found by Slack (1976). As is often the case, she found strong preferences among eastern North American trees, but none of the bryophytes occurred exclusively on one tree sp.

Wolf (1995) summarized the forces leading to presence and abundance of species in epiphytic bryophyte communities in the canopy of an Upper Montane Rain Forest, Central Cordillera, Colombia. He considered two

ways to look at these communities: emphasis on quality or quantity of preceding propagule supply; within community interactions such as competition. For the first of these, researchers have placed great importance on observed distribution patterns and high variability between epiphyte communities in seemingly identical habitats. But the great cover and biomass in these tropical montane rainforests suggests that competitive interactions may also be important. In his own study, Wolf found 120 bryophyte taxa (and 61 macrolichens). He recognized four community types from outer to inner canopy. Nevertheless, these four communities share many species and exhibit a species richness of about 100 taxa each. The inner canopy, with thick branches (21-80 cm diameter) had significantly fewer taxa per unit surface area, with an average of 1.72 taxa per dm² compared to 3.2 from the thinner middle canopy branches. Richness was even higher in the outer canopy, with 7.8 taxa per dm². If time were the most important factor, then the inner crown should have the highest number of species. Instead, one finds that the thick inner branches and trunks carry large patches of individual clones, suggesting competition through horizontal growth.

In the subtropical Tenerife, Canary Islands, González-Mancebo *et al.* (2003) described epiphytic bryophyte communities from five tree species in a laurel forest (Figure 41). Most of these bryophytes (37 species total) are **facultative epiphytes**, living on other substrates as well. And many are found on several tree species, with five being found on all five tree species. They further supported the observations that the species composition varies with bark characteristics, leeward vs windward exposure, height on tree, tree size, and degree of uprightness. Growth and life forms also relate to the moisture conditions of the bark.



Figure 41. Laurel forest on Tenerife, Canary Islands. Photo by Inkaro, through Creative Commons

In tropical forests that have high tree species richness, such host-tree relationships are absent; at the same height, one can expect to find mostly the same bryophytes in the same forest. However, in tropical forests with low tree species diversity, clear host-tree relationships may be observed. The best example is demonstrated by Cornelissen and ter Steege (1989; ter Steege and Cornelissen 1989) on dry evergreen forest in Guyana dominated by two tree species (*Eperua grandiflora* (rough-barked) or *E. falcata*) (wallaba, smooth-barked; Figure 42-Figure 43). Not surprisingly, the two tree species host different epiphytic bryophyte assemblages, with the rough bark of *E. grandiflora* supporting more epiphytes.



Figure 42. *Eperua falcata*, Guyana, showing smooth bark. Photo by Bernard Dupont, through Creative Commons.



Figure 43. *Eperua falcata*, a species that has smooth bark and inhabits dry sites. Photo by Hiobson, through Creative Commons.

Rudolph *et al.* (1998) examined host tree characteristics in a western Andean rainforest in Ecuador (Figure 44). Müller and Frahm (1998) elaborated on the epiphytic mosses in an Ecuadorian montane rainforest in the Andes. They found 65 species (24 mosses, 41 liverworts) on the ten trees they examined. They found no significant correlation between species number and branch diameter, branch exposure, or elevation. However, as bark pH increased, the number of epiphytic bryophyte species decreased.



Figure 44. Ecuador tropical rainforest in middle of Rio Tiguiono at Bataburo Lodge. Photo by Andreas and Christel Nöllert, with permission.

Thus, even in cases where host specificity is absent, certain characteristics seem to encourage or discourage bryophytes. As noted earlier, bark differences in the tropics can be important for some bryophyte species, but have little effect on bryophyte communities or species richness.

Host "trees" can also include tree ferns. Jaag (1943) examined the foliage renewal rate, leaf life, and epiphyte "involvement" on tropical tree ferns. Frahm (2003) described the meager studies on epiphytes on tree ferns. In Southeastern Brazil, he identified 142 species on *Cyathea* (Figure 45-Figure 46) and *Dicksonia* (Figure 47) trunks. Most of these seem to be chance occurrences, with only 20 species occurring on more than 10% of the fern trunks in the study. Vital and Prado (2006) found a species new to Brazil (*Ceratolejeunea dentatocornuta*; see genus in Figure 48) occurring on *Cyathea delgadii* (Figure 49-Figure 50). These were in a fragment of the Atlantic forest in the state of Sao Paulo. In total, the researchers found 35 bryophyte species, 12 of mosses and 23 of liverworts. Medeiros *et al.* (1993) reported epiphytes on *Cibotium* species (Figure 51) and *Sphaeropteris cooperi* (= *Cyathea cooperi*; Figure 52), both tree ferns, in a Hawaiian rainforest (Figure 53).



Figure 45. *Cyathea arborea* in Guadeloupe. In Brazil and elsewhere, this genus serves as substrate for epiphytic bryophytes. Photo by Patrice, through Creative Commons.



Figure 46. *Cyathea arborea*. In Brazil, trunks of this genus serve as substrates for epiphytic bryophytes. Photo by Xemenendura, through Creative Commons.



Figure 47. *Dicksonia antarctica*. In Brazil, this genus serves as substrate for epiphytic bryophytes. Photo by Fir0002-Flagstaffotos, with online permission.



Figure 48. *Ceratolejeunea cubensis*; *C. dentacornuta* was found as a new species on *Cyathea delgadii* in Brazil. Photo by Scott Zona, with permission.



Figure 49. *Cyathea delgadii*, host of the new species of liverwort *Ceratolejeunea dentacornuta*. Photo by Alcatron, through Creative Commons.



Figure 50. *Cyathea delgadii*, host of the new species of liverwort *Ceratolejeunea dentacornuta*. Photo by Alcatron, through Creative Commons.

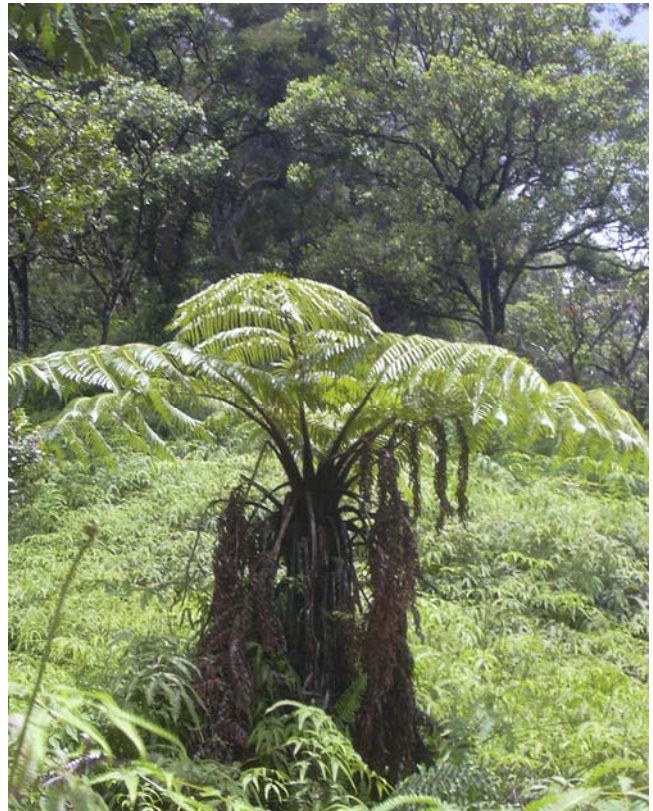


Figure 51. *Cibotium menziesii*; some members of this genus host bryophytic epiphytes in Hawaii. Photo by Forest and Kim Starr, through Creative Commons.



Figure 52. *Sphaeropteris cooperi*, host of bryophytic epiphytes in Hawaii. Photo through Creative Commons.



Figure 53. Spring rainforest stream with mosses, Hawaii. Photo by Jcklyn Baltazar, through Creative Commons.

Using a line-intercept method, Batista and Santos (2016) studied the epiphytic bryophytes in the Atlantic Forest of southeastern Brazil (Figure 54). They identified 71 taxa. The mean coverage did not vary significantly among the various phytophysionomies. Nevertheless, the species compositions were distinct among these phytophysionomies, but no cohesive or isolated groups emerged. There was, however, a correlation between bryophyte cover and tree DBH. Bark pH of the palm *Euterpe edulis* (Figure 55) and bark roughness of members of the tree fern family *Cyatheaceae* (Figure 49-Figure 50, Figure 52) also affected species composition.



Figure 54. Atlantic forest, Pernambuco coastal habitat, Camarigibe, Brazil. Photo by Leonardo Brito Uniemeik, through Creative Commons.



Figure 55. *Euterpe edulis* in Brazil. Bark pH of this species affects species composition of bryophytic epiphytes. Photo by Alex Popovkin, through Creative Commons.

In areas with many plantations and more than one host species, more specificity may present itself. For example, in Nigeria over 60% of *Octoblepharum albidum* (Figure 56) collections were from *Elaeis guineensis* (Egunyomi 1975, 1978), whereas *Calymperes palisotii* (Figure 57) prefers *Albizia saman* (Figure 58-Figure 59) over the relatively smooth, non-fissured bark of *Lagerstroemia* sp. (Figure 60-Figure 61) (Egunyomi & Olarinmoye 1983). Different agroforests [mango (Figure 62) and *Citrus* (Figure 63)] house unique bryophyte communities. Ezukanma *et al.* (2019) found that each of these two communities had 12 bryophyte species, but only five were common to both.



Figure 56. *Octoblepharum albidum*, one of the eight most common bryophytic epiphytes in the Amazon basin. Photo by Portioid, through Creative Commons.



Figure 57. *Calymperes palisotii* showing gemmae on leaf tips. Photo from Wilding *et al.* 2016, with permission.



Figure 58. *Albizia saman*, substrate for *Calymperes palisotii*. Photo by A. Gentry, MBG, through Creative Commons.



Figure 59. *Albizia saman* rough bark suitable for *Calymperes palisotii*. Photo by David Stang, through Creative Commons.



Figure 60. *Lagerstroemia speciosa* from India. The smooth bark of species of *Lagerstroemia* in Nigeria is not suitable for the moss *Calymperes palisotii*. Photo by Raju Kasambe, through Creative Commons.



Figure 61. *Lagerstroemia speciosa* bark from Hawaii, USA; smooth bark in this genus is not a preferred substrate for the moss *Calymperes palisotii* in Nigeria. Photo by Kim and Forest Starr, through Creative Commons.



Figure 62. Mango agroforest in India, a forest type that supports unique bryophyte communities in Nigeria. Photo from Bioversity International, through Creative Commons.



Figure 63. *Citrus* (orange plantation), a forest type that supports unique bryophyte communities in Nigeria. Photo by Hans Braxmeier, through Creative Commons.

Height on Tree

Andersohn (2004), working in central Guatemala, asked the question "Does tree height determine epiphyte diversity?" He listed the epiphytes, including the bryophytes. Many other studies have provided insight into this question.

Like epiphytes in other parts of the world, communities at the base, trunk, and crown differ due to light, moisture, and nutrients [Cornelissen & ter Steege 1986; Montfort & Ek 1990; Kürschner 1990 (studied only base and trunk)]. In some forests, the tree bases receive so little light that even bryophytes are unable to grow there. The branches, on the other hand, can have complex, dense growths that sometimes surround the entire branch like a winter muff (Figure 1) for warming one's hands. In the crown, high light intensity and dryness become limiting. For example, in the dry evergreen (wallaba – *Eperua falcata*; Figure 42-Figure 43) forest of Guyana, bryophytes and lichens on the canopy twigs of mature *Eperua* trees are predominantly of two types, the sun-tolerants and the pioneers (facultative epiphylls) (Cornelissen & ter Steege 1989). Many researchers follow the zones as described by Johansson (1974) (Figure 64-Figure 65).

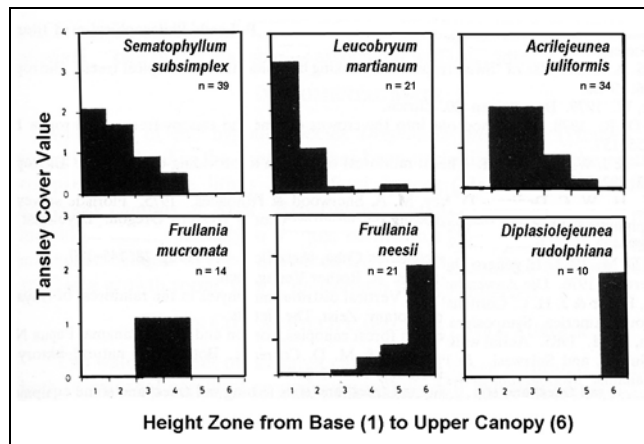


Figure 64. Vertical distribution (see Figure 65) of four moss and two leafy liverwort species in Guyana. Height zones are in Figure 65. Modified from Cornelissen & ter Steege 1989.

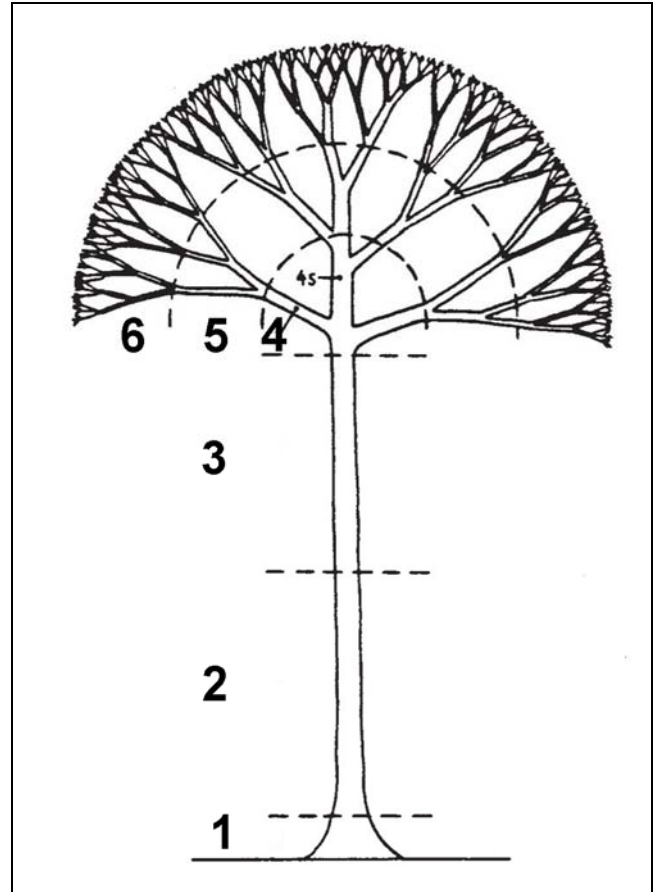


Figure 65. Epiphyte zones on a tree. Modified from Johansson 1974.

Zonation patterns occur from branch tips to center of the crown as well. Freiberg and Freiberg (2000) found that in the two lowland and two montane forests they studied in Ecuador (Figure 66), the epiphytic biomass per branch surface decreases from the center of the crown to the periphery.



Figure 66. Montane forests, Ecuador. Photo by Martin Zeise, through Creative Commons.

Pócs (1982) found that mosses dominate the base of the trunk, but leafy liverworts, especially the ever-present *Frullania* (Figure 67) and *Lejeuneaceae* (Figure 5, Figure 7-Figure 8), dominate the branches.



Figure 67. *Frullania* sp., a genus that dominates branches of tropical trees. Photo by George Shepherd, through Creative Commons.

In French Guiana (Figure 34), Gehrig-Downie *et al.* (2013) compared the diversity and vertical distribution of epiphytic liverworts between the lowland rainforest and the lowland cloud forest. These lowland cloud forests occur in river valleys with high air humidity and morning fog. This combination creates ideal conditions for epiphytic leafy liverworts. The researchers found a significantly higher species richness of these liverworts in the cloud forest and the species composition differed (Figure 68) in all six height zones (Figure 65).

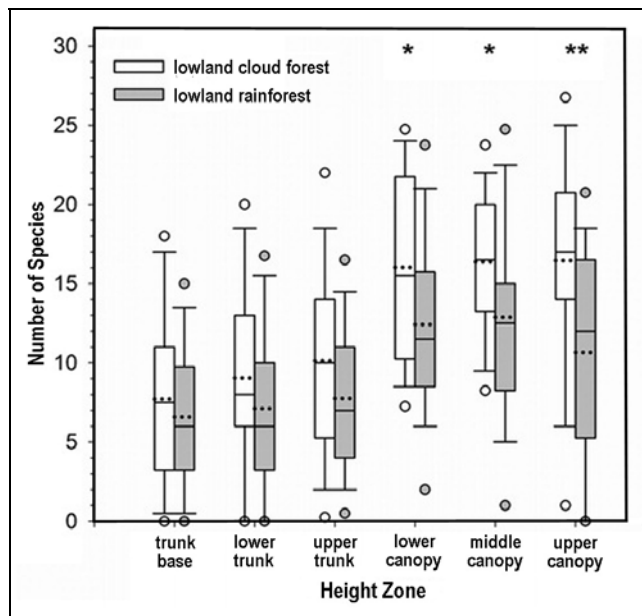


Figure 68. Number of epiphytic liverwort species in each tree height zone (see Figure 65) in the lowland cloud forest and lowland rainforest. $n=24$ trees per forest type. Boxes are upper and lower quartile, unbroken lines are medians, dotted lines are means, whiskers are 95 percentile, and circles are max and min. * $P<0.05$, ** $P<0.01$ for t-test differences. Modified from Gehrig-Downie *et al.* 2013.

The lowland cloud forests included more indicator species, particularly shade epiphytes and generalists that also occur in the montane forests (Gehrig-Downie *et al.* 2013). The lowland rainforest exhibited sun epiphyte indicators that characterize dry, open sites. At least in this case, liverwort species richness differs more between forest types than it does among elevation types. Furthermore, the lowland cloud forest may be more species-rich than are the montane rainforests. As is typical throughout most tropical habitats, the **Lejeuneaceae** (Figure 5, Figure 8, Figure 17, Figure 48) represents the largest family, with 95 species. This was followed by **Plagiochilaceae** (9 spp.; Figure 69) and **Frullaniaceae** (7 spp.; Figure 67). In the **Lejeuneaceae**, *Lejeunea* (Figure 70) had 14 species; *Ceratolejeunea* (Figure 48), *Cololejeunea* (Figure 71), and *Plagiochila* (Figure 69) each had nine species there.



Figure 69. *Plagiochila* sp. in the Neotropics. Photo by Michael Lüth, with permission.



Figure 70. Epiphyllous *Lejeunea* sp., a species-rich genus in the Neotropics. Photo by Bramadi Arya, through Creative Commons.



Figure 71. *Cololejeunea gracilis* var. *linearifolia* from Guadeloupe on leaf; *Cololejeunea* is a species-rich genus in the Neotropics. Photo by Tamás Pócs, with permission.



Figure 72. *Lagarostrobos franklinii*, a species that hosts lots of bryophytic epiphytes in Tasmania. Photo by Krzysztof Ziarnek, through Creative Commons.

Jarman and Kantvilas (1995), working on epiphytes of an old Huon pine (*Lagarostrobos franklinii*; Figure 72) in Tasmania, found 76 species of lichens, 55 of bryophytes, and 16 tracheophytes on that single tree. One factor accounting for the high diversity is that there is little overlap in species between the base and canopy taxa. Bryophytes dominate at the base, but lichens dominate in the more exposed crown. The bryophytes and lichens on these older trees build sufficient biomass peat on the branches that terrestrial tracheophytes are able to become established in the peat.

Oliveira and ter Steege (2013) used a standardized sampling method across the Amazon Basin (Figure 73) to describe the epiphytic bryophytes in five height zones from the forest floor to the canopy. They sampled eight canopy trees per locality, generating 3,104 records. They were able to identify 222 species and 39 morphospecies. As expected, the leafy liverwort family *Lejeuneaceae* (Figure 5, Figure 8, Figure 17, Figure 48) was the most common (55%), followed by the moss families *Calymperaceae* (Figure 9) (8%), *Leucobryaceae* (Figure 4) (4%), and *Sematophyllaceae* (Figure 99) (4%). Among these, 155 species occur in more than one locality, with 57 species considered to be specialists. In the canopy they found 29 species that are exclusive to the canopy.

Sporn *et al.* (2010) reported a record number of 146 epiphytic bryophyte species on eight canopy trees and eight trees from the understory of a submontane rainforest in Central Sulawesi, Indonesia (Figure 74). The trunks of canopy trees have significantly different species composition from that of the understory trees. Furthermore, 45% of the species are restricted to canopy tree crowns, whereas only 12% are restricted to the understory. This study emphasized that inventories of epiphytic bryophytes in a tropical forest should not only focus on canopy trees but also include the small understory treelets and shrubs, which may add at least 10% more species. A similar conclusion was reached by Krömer *et al.* (2007) in a study on tracheophytic epiphyte diversity in tropical submontane and montane forests.

Krömer *et al.* (2007) found that 90% of the tracheophytic epiphytes in the submontane and montane forests of the Bolivian Andes were represented in tree zones Z1-Z2 in the Johansson tree zones (Figure 65). Canopy tracheophytes were primarily orchids and ferns that had special adaptations to the frequent drought conditions. This vertical distribution responds to microenvironmental gradients of the tree, including light intensity, wind speed, and air temperature that increase with height, and moisture that decreases with height. But just what role do bryophytes have in their success?



Figure 73. Amazon rainforest aerial view in Brazil. Photo by Lubasia, through Creative Commons.



Figure 74. Sulawesi forest. Photo by T. R. Shankar Raman, through Creative Commons.

In lowland rainforests around Mabura Hill (Figure 75), Guyana, South America, Cornelissen and Gradstein (1990) reported 134 (52 mosses, 82 liverworts) bryophytes species. Of these, ~30% are **Lejeuneaceae** (Figure 5, Figure 8, Figure 17, Figure 48). Mountaineering techniques permit study of the forest canopy. There, 50% of the bryophyte species are exclusive to the canopy. The mixed forest has more exclusive species than does the dry evergreen forest, largely because of the outer canopy effect where xerophytic species occur. The canopy species in the dry evergreen forest have wider vertical distributions than do those in the mixed forest, a difference the researchers attribute to the more open canopy foliage in the dry evergreen forest.

Wolf (1994) examined epiphytic vegetation in the northern Andes (Figure 31). He restricted the bark type and sampled four full-grown forest trees at altitudinal intervals of ca 200 m from 1,000 to 4,130 m asl. The variation he found did not seem to relate to any environmental factor. Rather, as noted above, it seemed to relate to randomness in propagule supply. Nevertheless, ordination indicates that distribution patterns relate to altitude and height within the host tree. Interestingly, Oliveira and ter Steege (2015) found the same relationship in Amazonian lowland rainforest (Figure 73). Unlike many other studies, Wolf also found a relationship between the epiphytic vegetation and the host species, particularly for the host ***Brunellia occidentalis*** (see Figure 76-Figure 77), a

high altitude species with rapid growth. There is no indication of a relationship with chemical characteristics of suspended soil.



Figure 75. *Eperua rubiginosa* seedlings, Mabura Hill Forest Reserve, Guyana. Photo by Hans ter Steege, through Creative Commons.



Figure 76. *Brunellia comocladifolia*; *B. occidentalis* is an epiphyte host at high altitudes in the Andes. Photo by Yolanda Leon, through Creative Commons.



Figure 77. *Brunellia goudotii* in Colombia; *B. occidentalis* is an epiphyte host at high altitudes in the Andes. Photo by Alvaro Neira, through Creative Commons.

Oliveira *et al.* (2010) noted that, like tracheophytes, bryophytes demonstrate a species gradient from the base to the upper canopy of the host trees. They set out to test the role of niche assembly on a regional scale. They sampled six height zones on several trees in each of three lowland forests of the Guianas (Figure 34) and found that height zone was relatively consistent in the three localities, despite distances up to 640 km, and that that consistency was greater than among communities within the height zones of a single tree (30-50 m in height). More than half (57%) of the species exhibited a height zone preference.

Overall, Oliveira (2010) identified 225 species and 38 morphospecies of Amazonian basin epiphytic bryophytes. As we might expect, the leafy liverwort family **Lejeuneaceae** was the most species-rich family (55% of species). Among the mosses, the most common families were **Calymperaceae** (8%), **Leucobryaceae** (4%), and **Sematophyllaceae** (4%). All four of these families occurred in all 9 sampling locations. The most common species was the leafy liverwort *Cheilolejeunea rigidula* (see Figure 78), followed by *Ceratolejeunea cornuta* (Figure 79), *Octoblepharum pulvinatum* (Figure 80), *Octoblepharum albidum* (Figure 56), *Archilejeunea fuscescens* (see Figure 81), *Sematophyllum subsimplex* (Figure 82), *Lopholejeunea subfusca* (Figure 83), and *Symbiezidium barbiflorum* (see Figure 84). These eight species accounted for 21% of the known species in the study.

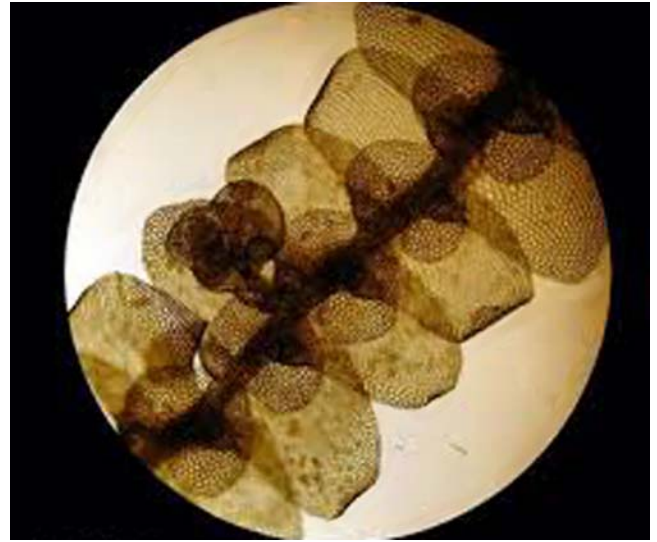


Figure 79. *Ceratolejeunea cornuta*, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Michaela Sonnleitner, with permission.



Figure 80. *Octoblepharum pulvinatum* (light green), one of the eight most common bryophytic epiphytes in the Amazon basin, and *Syrropodon* on tree bark in the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.



Figure 78. *Cheilolejeunea* sp. from the Neotropics; *C. rigidula* is the most common epiphytic bryophyte in the Amazon basin. Photo by Michael Luth, with permission.



Figure 81. *Archilejeunea olivacea*; *A. fuscescens* is one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by John Braggins, through Creative Commons.



Figure 82. *Sematophyllum subsimplex*, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Yelitza Leon, through Creative Commons.



Figure 83. *Lopholejeunea subfusca*, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Yang Jiadong, through Creative Commons.



Figure 84. *Symbiezidium* sp.; *S. barbiflorum* is one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Hermann Schachner, through Creative Commons.

Oliveira (2010) found that a total of 155 species occurred in more than one locality, and of these 57 were considered to be specialists (37%), whereas 98 (63%) were considered generalists. The specialists were typically found at the extremes of the gradient, either in zone 1 or zone 6. Only 8 seemed to be specialists in other tree zones. Oliveira concluded that the structure of the communities fit the Neutral Model of Biodiversity and Biogeography, *i.e.*, being there by random recruitment from the local environment. The distribution of the species appears to be influenced by two processes. On a local scale, the interaction between the environment and local abundance provide the greatest influence. Within the Amazon basin, the abundance of the species in the **metacommunity** (sum of all communities sampled in localities) are the primary influence. Furthermore, the frequency of long-distance dispersal increased with the height of the zone in the tree. What seems strange is that the greatest genetic distance occurs between the canopy and subcanopy.

In the constant clouds of the dense montane **ombrophilous** (capable of withstanding or thriving in presence of high rainfall) forest (1,000 to 1,500 m asl) in southern Brazil (Figure 85), Santos *et al.* (2018) characterized six vertical zones on 28 trees and identified 96 species of bryophytes in 31 families. The leafy liverwort family **Lejeuneaceae** (Figure 5, Figure 7-Figure 8) was the most species-rich family, followed by **Frullaniaceae** (Figure 67). Liverworts predominated. Species diversity was high, ranging from $H' = 2.6$ to $H' = 4.1$, with high abundances. Of the 28 trees sampled, across this elevation range, the species composition was similar, with only two differing by more than 50%. Bryophyte cover ranged from 3.04% (2 m high to first branches; epiphylls) to 8.97% (0.0-0.5m) in the six phorophyte zones.

Tree Base

In the rainforests, the least light reaches the bases of the great trees (Pócs 1982). At the same time, the bases have the highest humidity in the forest. The bole height of dense bryophyte growth is limited by humidity and the physical condition of the bark, but where it is extremely wet it can reach as high as the first main branches, which may reach 8-10 m high (Richards 1954; Pócs 1982). More typically, it reaches up to 1-3 m, being limited by humidity that sinks to 60% during dry periods (Pócs 1974).



Figure 85. Brazilian southern highlands. Photo by Cecicilio, through Creative Commons.

On tropical tree bases one is likely to find **mats** and **wefts** of various *Thuidium* (Figure 86) species, intermixed *Fissidens* (Figure 87), and the leafy liverworts in *Lejeuneaceae* (Figure 5, Figure 8, Figure 17, Figure 48) and small turfs of mosses in *Orthotrichaceae* (Figure 25) (Gradstein & Pócs 1989). More suitable, porous bark often supports growths of the mosses *Leucobryum* (Figure 4), *Leucophanes* (Figure 9), and *Calymperes* (Figure 88). Farther up one might find **turfs** of the mosses *Dicranaceae* such as *Leucoloma* (Figure 89). As the **wefts** and **turfs** grade away from the base, one can find the **feather** type forming horizontal shelves on the bole (Figure 90) (Gradstein & Pócs 1989). The **dendroid**, **feather**, and **bracket** forms are specialists on the more narrow stems of small trees and branches of shrubs in this low-light zone, but they can also be found at the base (Pócs 1982). These include the mosses *Lopidium* (Figure 91) and *Pinnatella* (Figure 92) on all continents with tropical forests.



Figure 86. *Thuidium cymbifolium* with capsules, in a genus that can be found on some tree bases in tropical rainforests. Photo by Li Zhang, with permission.



Figure 87. *Fissidens serratulus*, in a genus that occurs on tree bases in tropical rainforests. Photo by Jonathan Sleath, with permission.



Figure 88. *Calymperes tenerum*, in a genus that occurs on porous bark of tree bases. Photo from the Auckland Museum, through Creative Commons.



Figure 89. *Leucoloma* sp. in the Neotropics, a genus that occurs above the tree base in tropical rainforests. Photo by Michael Lüth, with permission.



Figure 90. *Neckera pennata*, demonstrating shelf formation. Photo by Janice Glime.



Figure 91. *Lopidium concinnum*. Photo by David Tng, with permission.



Figure 92. *Pinnatella* sp. in Bhutan. Photo by David Long, with permission.

In the lowland rainforest of Guyana (Figure 93), Cornelissen and ter Steege (1989) found that the tree base community is characterized by the abundance of pleurocarpous mosses. In the wet, very shady habitats of tree bases these pleurocarpous species include **pendulous** and **dendroid** mosses in the **Neckeraceae** (Figure 95-Figure 96) and **Pterobryaceae** (Figure 113) (Pócs 1982). In Asia, these include the mosses *Homaliodendron* (Figure 94) and *Neckeropsis* (Figure 95-Figure 96), both in **Neckeraceae**; in Africa one finds the mosses *Renauldia* and *Hildebrandtiella* (Figure 97) in the **Pterobryaceae** and *Porotrichum* (**Neckeraceae**; Figure 98). In the Neotropics, *Neckeropsis disticha* (Figure 95) and *N. undulata* (Figure 96) are ubiquitous. The mosses *Sematophyllum* (Figure 99) and *Taxithelium* (Figure 114) are likewise common in this synusia, with ~100 species in Vietnam, 60 in East Africa, and 50 in Cuba.



Figure 93. Forest at Angoulême, French Guiana (Guyana). Photo by M. Wilkinson, E. Sherratt, F. Starace, and D. J. Gower, through Creative Commons.



Figure 94. *Homaliodendron flabellatum*, in a genus that occurs on tree bases of wet, shady tropical habitats in Asia. Photo by Yao, through Creative Commons



Figure 95. *Neckeropsis disticha*, a species that occurs on tree bases of wet, shady Neotropical habitats. Photo by Piers Majestyk, through Creative Commons.



Figure 96. *Neckeropsis undulata*, a species that occurs on tree bases of wet, shady Neotropical habitats. Photo by Scott Zona, with permission.



Figure 98. *Porotrichum bigelovii*, in a genus that occurs on tree bases of wet, shady tropical habitats in Africa. Photo from Calbryos, with permission through Paul Wilson.



Figure 97. *Hildebrandtiella guyanensis*, in a genus that occurs on tree bases of wet, shady tropical habitats in Africa. Photo by Claudio Delgadillo Moya, with permission.



Figure 99. *Sematophyllum substrumulosum*, in a genus that occurs on tree bases of wet, shady Neotropical habitats. Photo by James K. Lindsey, with permission.

In Costa Rica, Holz *et al.* (2002) documented the diversity, microhabitat differentiation, and distribution of life forms in the tropical upper montane *Quercus* forest [*Q. copeyensis* (Figure 100), *Q. costaricensis* (Figure 101)], using seven freshly fallen trees. They were surprised to find that not only is the tree base bryophyte community distinct from that of the rest of the tree, it is fundamentally the same as that of the forest floor! They also noted the importance of the understory as bryophyte habitat. On **lianas** (vines), poles, twigs on shrubs, ferns, and palms they found 65 species. More details of the Holz *et al.* study are in the subchapter Tropics: Altitude.



Figure 100. *Quercus copeyensis*, a species whose tree base bryophytes match those of the forest floor. Photo through Creative Commons.



Figure 101. *Quercus costaricensis*, a species whose tree base bryophytes match those of the forest floor. Photo by Stan Shebs, through Creative Commons.

Further descriptions of the epiphyte bryophyte habitat can be found in Richards (1954) from Guiana (Figure 34), Iwatsuki (1960) from southern Japan, and Tixier (1966) from South Vietnam.

Equihua and Equihua (2007) examined spatial distributions of *Bryopteris filicina* (Lejeuneaceae; Figure 102) on tree trunks in Chiapas, Mexico (Figure 103). They found it to be over-represented on *Ampelocera hottlei* (Figure 104), *Brosimum alicastrum* (Figure 105), and *Guarea glabra* (Figure 106), all species with smooth bark. Its distribution was determined by height on the tree, bark texture, and orientation, preferring smooth texture and a north-facing orientation.



Figure 102. *Bryopteris filicina* in the Neotropics. Photo by Michael Lüth, with permission.



Figure 103. Selva Lacandona in Chiapas, Mexico. Photo by Marrovi, modified, through Creative Commons.



Figure 104. *Ampelocera hottlei* bole showing smooth bark, a tree preferred by bryophytes. Photo by Indiana Coronado, through Creative Commons.



Figure 106. *Guarea glabra* showing smooth bark, a tree preferred by bryophytes. Photo from Smithsonian Institution, through public domain.

Upper Trunk

The upper trunks have mostly appressed species (Schofield 1985, pp. 313-314). These are most commonly leafy liverworts such as *Frullania* (Figure 67) and *Lejeuneaceae* (Figure 5, Figure 8, Figure 17, Figure 48) (Pócs 1982). Among the mosses one can find **smooth mats** and thread-like *Sematophyllaceae* (Figure 99) again, as well as *Hypnaceae* (Figure 107) and *Mitthyridium* (Figure 108), again being appressed.

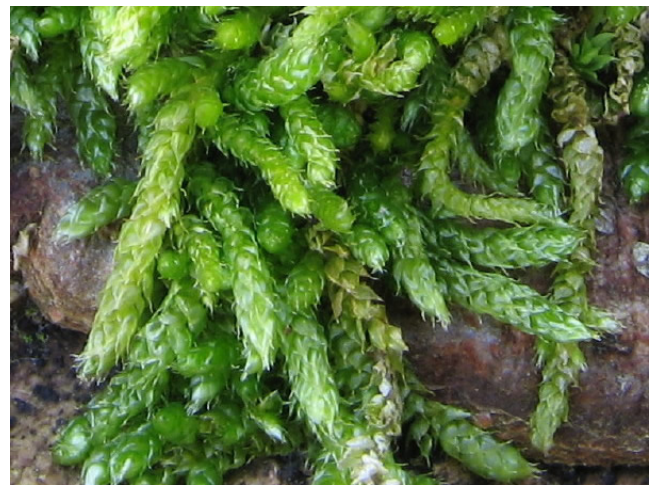


Figure 107. *Hypnum cupressiforme* var. *heseleri*, a smooth mat former. Photo by Robin Stevenson, with permission.



Figure 105. *Brosimum alicastrum* tree base showing smooth bark, a tree preferred by bryophytes. Photo by David Stang, through Creative Commons.

Kürschner and Parolly (1998c) used the **Braun-Blanquet method** (system using cover-abundance classes; Poore 1955) to describe the various associations on tropical rainforest tree boles. The distribution patterns of the trunk-epiphytic vegetation can be generalized pantropically. Three alliances fall into two orders. Their distribution is correlated to structural parameters of the phorophyte stands and to **isothermic** (equal temperature) intervals: tropical lowland and submontane alliances (20-27°C mean annual temperature); subtropical and montane alliances of the montane rain- and cloud forests (12-20°C); temperate, boreal to subalpine alliances of elfin forests and ericaceous woodlands ((5)8-12°C). A fourth unit (<8°C) includes the

Afro-subalpine *Syntrichion cavallii* (see Figure 109), mostly known outside the moist tropics and typical of the subpáramo vegetation.



Figure 108. *Mitthyridium micro-undulatum*, among the genera one can find on the upper trunks. Photo by Jan-Peter Frahm, with permission.



Figure 109. *Syntrichia* sp., *Syntrichia cavallii* is part of an Afro-subalpine association that lives in elfin forests with low temperatures. Photo by J. C. Schou, with permission.

Lower Branches

The lower, thick canopy branches are typically inhabited by large **mats** of robust epiphytic bryophytes such as *Plagiochila* (Figure 69), *Bazzania* (Figure 102, Figure 110), *Macromitrium* (Figure 111), and others (Cornelissen & ter Steege 1989). Using mountaineering techniques, Cornelissen and ter Steege sampled the *Eperua* trees [*Eperua grandiflora* and *E. falcata* (Figure 42-Figure 43)] in the dry evergreen forest of Guyana (Figure 42) from the base to the highest canopy twigs. This revealed a clear vertical distribution pattern of species and life forms for bryophytes. The upper canopy twigs are particularly species rich with both sun epiphytes and pioneers (facultative epiphylls).



Figure 110. *Bazzania* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 111. *Macromitrium* sp. from the Neotropics. Photo by Michael Lüth, with permission.

Epiphyllous bryophytes, predominantly leafy liverworts in the *Lejeuneaceae* (Figure 5, Figure 8, Figure 17, Figure 48), abound in this lower branch zone, but also occur in abundance in the forest understory (Gradstein & Pócs 1989), in both cases living out of the damaging and desiccating reaches of the sun. The general trend observed for epiphylls is a reduction of species richness from the understory to the canopy (see Montfoort & Ek 1990), while species richness of epiphytes usually increases. These epiphyllous communities are discussed in the subchapter Tropics: Epiphylls.

Twigs

Wolf (1993a, b, c, 1995) described the changes in epiphytic bryophyte community structure of the montane forest, from the canopy twigs to the thickest lower canopy branches, in admirable detail. The lower branches and terminal twigs (Figure 112) of lowland forests support the pendent **Meteoriaceae** (Figure 112) and **Pterobryaceae** (Figure 113), provided it is sufficiently humid, and also the ever-present leafy liverworts **Frullania** (Figure 67) and **Lejeuneaceae** (Figure 5, Figure 8, Figure 17, Figure 48) (Pócs 1989). Here one finds **Neckeraceae** (Figure 95-Figure 96) and **Pterobryaceae** such as **Lopidium** (Figure 91) or **Pinnatella** (Figure 92), or others that are more specific to certain continents (Pócs 1982). **Sematophyllum** (Figure 99) and **Taxithelium** (Figure 114) reach their peak here. Farther up on the main branches, bryophytes must withstand high light and desiccation. There, dense mats occur, including the mosses **Cryphaeaceae** (Figure 115), **Erpodiaceae** (Figure 116-Figure 117), **Orthotrichaceae** (Figure 25), and **Sematophyllaceae** (Figure 99), as well as the liverworts **Frullania** and **Lejeuneaceae** (Figure 5, Figure 8, Figure 17, Figure 48). For those of us from the north temperate and boreal zones, only **Orthotrichaceae** and a few **Frullania** and **Lejeuneaceae** taxa are familiar.



Figure 112. *Pseudobarbella mollissima*, a pendent moss in Japan. Photo by Janice Glime.



Figure 113. *Hildebrandtiella guyanensis* (Pterobryaceae) in the Neotropics. Photo by Michael Lüth, with permission.

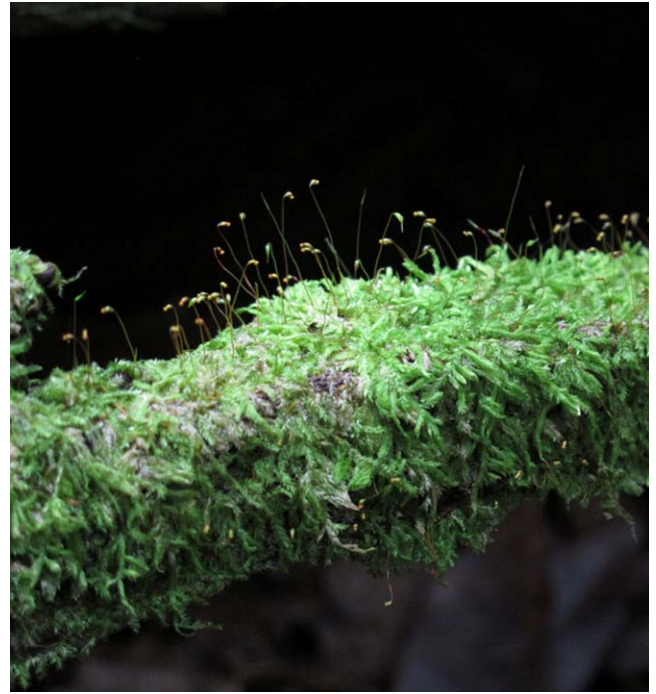


Figure 114. *Taxithelium planum*. Photo by Scott Zona, with permission.



Figure 115. *Cryphaea jamesonii* (Cryphaeaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 116. *Aulacopilum abbreviatum* forming mats on a tree in Bareilly India. Photo by Michael Lüth, with permission.



Figure 117. *Aulacopilum abbreviatum* forming a dense **mat** in Bareilly India. Photo by Michael Lüth, with permission.

Several species found on the fine canopy twigs are not restricted to this habitat but also occur lower down in the forest on the upper trunks or on living leaves in the forest understory (Cornelissen & ter Steege 1989). These species are considered pioneer species of the rainforest, well adapted to growth on open, unstable substrates. Most of them are small **Lejeuneaceae** (Figure 5, Figure 8, Figure 17, Figure 48) and copiously reproduce by vegetative propagules.

Romero (1999) found the most abundant **pendent** bryophytes on the thin branches (<1 cm diameter). The highest biomass per unit substrate occurred on branches of shade-tolerant species.

Canopy

The canopy, especially the outer canopy, can be a very different and stressful habitat in the forest. It is exposed to the full force of the wind. But based on turbulence analysis of two Amazon rainforest canopies (Figure 14, Figure 73), Kruijt *et al.* (2000) reported a sharp daytime attenuation of turbulence in the top third of the canopies. Thus, within the canopy there is very little air movement. Their hypothesis is that "the upper canopy air behaves as a plane mixing layer." This suggests that tropical rainforest canopies differ from other forests where there are rapid, coherent downward sweeps that penetrate the lower canopy. This penetration does not occur in these Amazonian rainforests. Rather, there is strong heat absorption by the canopy leaves near the top. The weak turbulence is unable to destroy the temperature gradient that is present through the large canopy depth. The inversion is likely to be maintained by strong heat absorption in the leaves concentrated near the canopy top, with the generally weak turbulence being unable to destroy the temperature gradients over the large canopy depth.

Sillett (1991) studied canopy bryophyte communities of six mature *Ficus aurea* (Figure 118-Figure 119) trees to elucidate the canopy bryophyte community and compare microhabitats. He divided these into three intact cloud forest and three isolated trees in Costa Rica. He used hemispherical canopy photography to compare light in the crowns, determining that the interior crowns of isolated trees were twice as bright as those in the intact forest. Isolated trees had lower species richness and life-form

diversity. He found 41 species of mosses on the intact forest trees compared to only 29 on the isolated trees, with 50 species in total. The bryophytes on the forest trees are dominated by **pendants**, **fans**, **wefts**, and **tall turfs**, whereas the isolated trees have more **short turfs**. As in other studies, variation of bryophyte communities is greater within a single tree than among trees. Furthermore, the among-tree variation is greater in the forest than among isolated trees.



Figure 118. *Ficus aurea*, a species that supports many more epiphytes when in the forest than when isolated in the open. Photo by Forest and Kim Starr, through Creative Commons.

Gradstein (2006) described the lowland cloud forest of French Guiana (Figure 120) (in moist river valleys below 400 m asl) where the climate differs from that of the mixed lowland rainforest, but differs by the frequent presence of fog and a large presence of epiphytes, especially liverworts. This forest has species richness of epiphytic liverworts that is similar to that at 2,000 m asl in the Andes and exhibits three times the richness of the Amazonian lowland forest (Figure 14, Figure 73). The moisture counterbalances the high temperatures, permitting the large diversity. The taxonomic composition and abundance differ from those in the tropical montane cloud forest. In the lowland cloud forest, asexual reproduction and dispersal are significantly more common in the canopy than in the forest understory. These canopy species have significantly wider ranges than that found among understory species. Gradstein suggested that these wider ranges are due to long-range dispersal by spores.



Figure 119. *Ficus aurea* in Costa Rica, showing epiphytes on the buttresses. Photo by Has Hillewaert, through Creative Commons.



Figure 120. Canopy in a lowland cloud forest of French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Logs and Rotten Wood

Where lumbering or wind and hurricane disturbances occur, logs become a visible feature of the landscape (Figure 121). They also result from the normal aging and death of a tree. These logs provide a different habitat, especially in the **epixylic stage** (after bark is lost; Figure 122), than that of tree trunks.



Figure 121. Illegal export of rosewood logs from Madagascar. Photo by Erik Patel, through Creative Commons.



Figure 122. Decorticated log with epixylic bryophytes. Photo from UuMUfQ, through Creative Commons.

Winkler (1976) conducted some of the earliest studies of tropical bryophytes on rotten wood. Frahm (2003) compared the taxa on rotten wood in the tropics. This is the primary available substrate in lowland forests due to the heavy cover of leaf litter elsewhere on the forest floor. Logs usually are inhabited by **Sematophyllaceae** (Figure 99), **Hookeriaceae** (Figure 131), and **Leucobryaceae** (Figure 4) among the mosses. At Monteverde, one can also find *Pyrrhobryum spiniforme* (Figure 123) (Gradstein *et al.* 2001). In the cloud forest of Monteverde, Costa Rica (Figure 124), one can find the bryophytes on logs that can differ from these (see subchapter Tropics: Altitude, part 2).



Figure 123. *Pyrrhobryum spiniforme* in Hawaii. Photo by Alan Cressler, with permission.



Figure 124. Monteverde cloud forest, Costa Rica. Photo by Haakon S. Krohn, through Creative Commons.

The rotten wood of moist tropical montane forests supports a rich bryophyte flora. Such logs on Mt. Meru and the Usambara Mountains in Tanzania (Figure 125) supported 102 taxa of bryophytes on logs (86 mosses, 16 liverworts), including 71 taxa in 51 20x20 cm plots. (Mattila & Koponen 1999). Cornelissen and Karssemeijer (1987) presented a scale to determine the decomposition stage of the wood: 1 – knife does not penetrate, 2 – penetrates one centimeter, 3 – penetrates several centimeters, 4 – penetrates to the handle. (See also Frahm 2003 for its use in the tropics.)

In Neotropical Puerto Rico, Sastre-de Jesús (1992) found that **Lejeuneaceae** (Figure 5, Figure 7-Figure 8) and **Calymperaceae** (Figure 9, Figure 88) dominated the logs with bark intact. Softwood logs frequently had *Taxithelium planum* (Figure 114) and *Isopterygium tenerum* (Figure 126). Bryophytes on heavily decayed logs tended to have species with higher water requirements, presumably due to the relatively constant water content of these logs.



Figure 125. Western Usambara Mountains, Tanzania. Photo by David Ashby, through Creative Commons.



Figure 126. *Isopterygium tenerum*, a species that occupies softwood logs in Puerto Rico. Photo by Scott Zona, through Creative Commons.

Rotten logs and rotting wood with bryophytes are able to retain good moisture (Laman 1995). This in turn provides a suitable and important substrate for the germination of seeds such as *Ficus crassiramea* subsp. *stupenda* (Figure 127-Figure 128).



Figure 127. *Ficus crassiramea* subsp. *stupenda*, a species that germinates on bryophyte-covered logs in the tropics. Photo by Pia Tan, through Creative Commons.



Figure 128. *Ficus crassiramea* subsp. *stupenda*, a species that germinates on bryophyte-covered logs in the tropical rainforest. Photo by Reuben C. J. Lim, through Creative Commons.

Parolly and Kürschner (2005) reported that under the relatively stable climatic conditions of tropical montane forests, the decay process is predictable. These conditions favor the **weft** and **mat** life form, following **perennial stayers**, a succession similar to that of the trunk epiphytic communities. Flood disturbance is more likely to favor species that are **dendroid** and **mat-forming shuttle species** that utilize a diaspore bank to return after flooding. In dry conditions, species are more likely to be **short-turf-forming colonists**. Shady sites are most suitable for **wefts**, giving them greater exposed surface area to take advantage of the low light conditions.

In the remnant Atlantic forest (seasonal coastal deciduous forest; Figure 129) of Brazil, Germano and Pôrto (1996, 1997) found 35 epixylic species of bryophytes. These comprised 11 families of mosses [*Calymperaceae* (Figure 9, Figure 88), *Pilotrichaceae* (Figure 130), *Fissidentaceae* (Figure 87), *Hookeriaceae* (Figure 131), *Hypnaceae* (Figure 132), *Leucobryaceae* (Figure 4), *Leucomiaceae* (Figure 133), *Orthotrichaceae* (Figure 25), *Plagiotheciaceae* (Figure 134), *Sematophyllaceae* (Figure 99), *Thuidiaceae* (Figure 135)] and 5 families of liverworts [*Aneuraceae* (Figure 136), *Frullaniaceae* (Figure 67), *Geocalycaceae* (Figure 137), *Plagiochilaceae* (Figure 69), *Radulaceae* (Figure 32)]. Note the absence of *Lejeuneaceae*. They related the species composition to the decomposition stage of the substrate (Germano & Pôrto 1997).



Figure 129. Remnant Atlantic forest, Brazil. Photo by Leandro Pereira Chagas, through Creative Commons.



Figure 130. *Pilotrichella ampullacea* (*Pilotrichaceae*), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Jan-Peter Frahm, with permission.

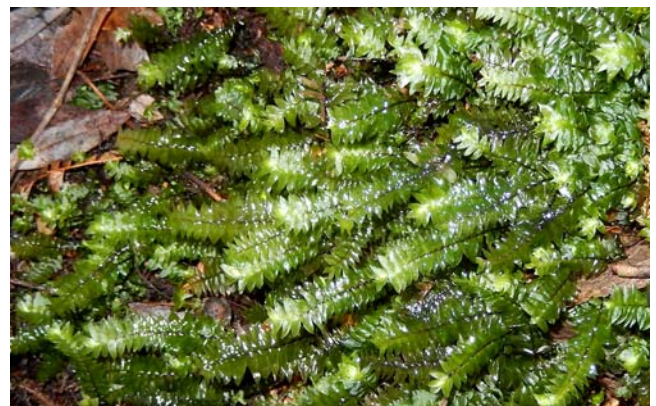


Figure 131. *Cyathophorum bulbosum* (*Hookeriaceae*), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Peter Woodard, through Creative Commons.



Figure 132. *Hypnum curvifolium* (Hypnaceae) with capsules on rock, in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Bob Klips, with permission.



Figure 135. *Pelekium cf. gratum*. Photo by Shyamal L., through Creative Commons.



Figure 133. *Leucomium strumosum* (Leucomiaceae), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Claudio Delgadillo Moya, with permission.

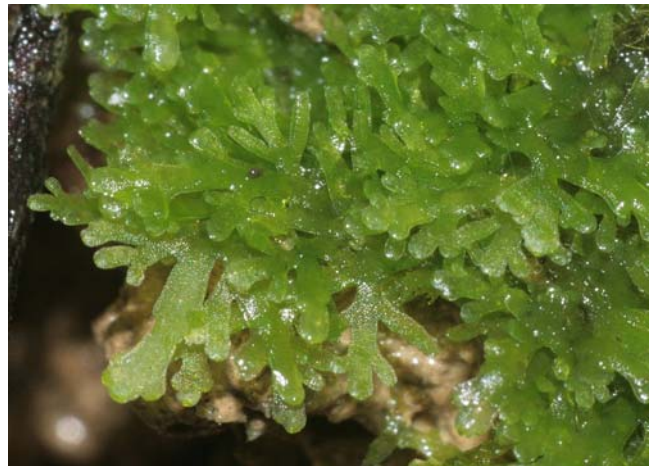


Figure 136. *Riccardia multifida* (Aneuraceae), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Hermann Schachner, through Creative Commons.



Figure 134. *Plagiothecium undulatum*; the Plagiotheciaceae, a family represented in a remnant of the Atlantic Forest. Photo by J. C. Schou, with permission.



Figure 137. *Geocalyx graveolens* (Geocalycaceae), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Michael Lüth, with permission.

In forest fragments in the Atlantic forest (Figure 129) of northeastern Brazil, Silva and Pôrto (2009) used 100 m transects and small (<100 ha), medium (100-500 ha), and large (>500 ha) fragments to examine fragmentation and

edge effects on bryophytes growing on decaying wood. They identified 99 species of epixylic bryophytes (52 liverworts, 47 mosses); liverworts barely predominated here. They found that fragment size was important in determining composition, richness, diversity, and abundance on epixylic substrata. Furthermore, species richness, coverage, and shade tolerance did not correlate with the distance from forest edge. Rather, edge effects seemed to be non-linear, extending beyond 100 m from the forest edge.

In Pernambuco, Brazil, Germano and Pôrto (1996) described the dominant bryophytes in several community types. They found that *Cololejeunea sicaefolia* (see Figure 138), *Lejeunea quinque-umbonata* (Figure 139), both in the *Lejeuneaceae*, and *Riccardia* spp. (Figure 136) are exclusively **epixylic** in their study area.



Figure 138. *Cololejeunea subcristata*; *C. sicaefolia*, a leafy liverwort that occurs exclusively on decaying wood in the Pernambuco, Brazil, study area. Photo by Scott Zona, through Creative Commons.



Figure 139. *Lejeunea quinque-umbonata*, a leafy liverwort that occurs exclusively on decaying wood in the Pernambuco, Brazil, study area. Photo by Elena Reiner-Drehwald.

Sampling

Many bryophytes grow high in the canopy and this provides a particular challenge for collection. Popular recent methods include rope-climbing (Figure 140) (Perry 1978; Whitacre 1981; Cornelissen & ter Steege 1986) and bow-and-arrow techniques (Dial & Tobin 1994). These methods can even be used to collect the tiny leafy liverworts that hide among the larger bryophytes and tracheophytes. Tweedie and Bergstrom (1995) developed a

hierarchical approach for bryophytic epiphytes that could handle their spatially complex ecosystems.



Figure 140. Rope-climbing to sample the canopy of a lowland rainforest in the Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

Pardow *et al.* (2012) concluded that bryophyte life-form analysis of the canopy can be accomplished from the ground in the lowland rainforest of French Guiana (Figure 34). When this is the case, life forms could be used easily to indicate functional diversity.

Several sampling techniques for estimating abundance of non-vascular epiphytes, including bryophytes, have been developed over the past decade. The efficacy of those techniques, however, has never been investigated. Lovai *et al.* (2012) compared three protocols for sampling epiphytic bryophytes in tropical montane rainforests. They examined ladder quadrats, 10 x 10 cm quadrats at intervals of 40 cm, and a 10-cm-wide strip around the stem. The use of 10 x 10 cm quadrats at intervals of 40 cm proved to be the most effective and efficient sampling method for quantifying bryophyte cover and demonstrated a typical species-area curve (Figure 141).

Bryant *et al.* (1973) used **R-mode analysis** (species x species) and **Q-mode analysis** (principal component analysis for linear discriminant analysis) (Lee *et al.* 2017) of area x area to compare the distributional patterns of 155 species of leafy liverworts in the Luquillo Mountains of Puerto Rico (Figure 142). They compared high altitude with low-altitude areas, shaded, moist habitats with open, more exposed habitats, and disturbed, low-elevation habitats with less disturbed habitats at all elevations. R-mode and Q-mode produced nearly identical distribution patterns. Therefore, either method can be used to determine which species are the best indicators of habitat differences.

A technique that has been used in ecological studies in several ecosystems is that of recording **morphospecies** (species forms). This permits the researchers to use a team of novices and accomplish a wide survey in a short time (Gradstein *et al.* 2003). Using the technique for bryophytes, lichens, and tracheophytes, but not epiphylls, they estimated that they could inventory one hectare of tropical rainforest in two weeks. No identifications were attempted, enabling a team of six with three specialists (bryophytes, lichens, tracheophytes) and three assistants to accomplish the survey.

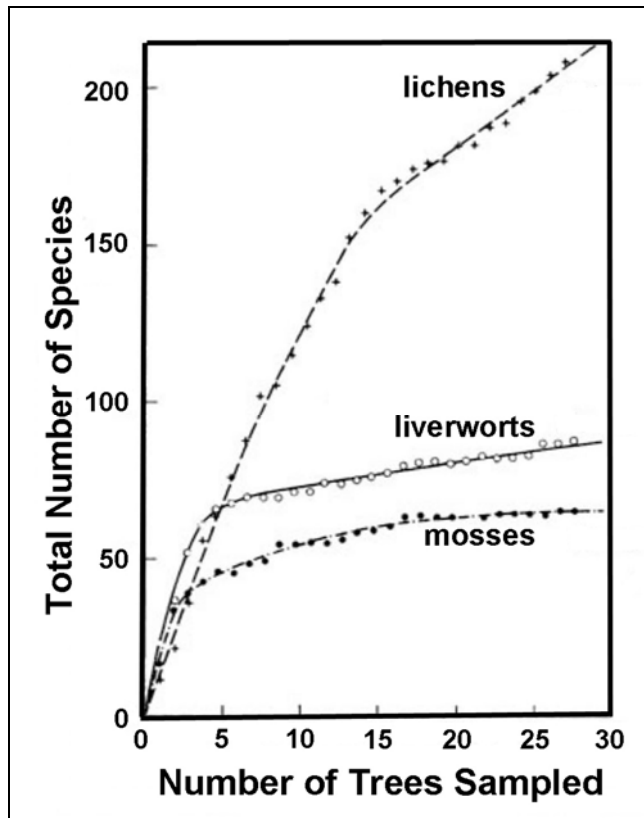


Figure 141. Species-area curve for epiphytic bryophytes and lichens in a lowland rainforest of French Guiana, based on Montfoort & Ek 1990.



Figure 142. El Yunque National Forest, Luquillo Mountains, Puerto Rico. Photo by Kai Griebenow, through Creative Commons.

Gradstein *et al.* (2003) developed a standard protocol of recording morphospecies (species forms) for rapid and representative sampling of epiphyte diversity of one hectare of tropical rainforest. Based on species-accumulation curves they found that inventories of 5 whole trees, using standard plots in all height zones, may be sufficient to sample 70-80% of the diversity of the epiphytic bryophytes of the forest. For vascular epiphytes and epiphytic lichens, however, more trees must be sampled. Using the protocol, the bryophyte inventory of one hectare can be

accomplished in two weeks by a team of one specialist and one field assistant. The results obtained by means of the standard protocol have been used for making comparisons of bryophyte species richness along elevational gradients (Gehrig-Downie *et al.* 2013) and along disturbance gradients (Gradstein & Sporn 2010). A standardized technique also permits comparisons between locations (countries) and hopefully even among researchers.

Quadrats

Nadkarni (2000) established "cylindrats" that she used to track colonization. In a lower montane cloud forest, Monteverde, Costa Rica, she used photography to track the colonization in these epiphytic plots. She also wrapped a clear acetate sheet around the branch, then placed a second clear sheet with a matrix of 100 dots (10x10). Using five random locations around the branch segment she counted the number of dots that touched epiphytes. These counts were converted to percent cover.

Affeld *et al.* (2008) used single samples (30 x 25 cm) from 96 epiphyte assemblages located on inner branches of 40 northern rata (*Metrosideros robusta*; Figure 143-Figure 144) trees to show that epiphytes are important in determining community structure on South Island, NZ.



Figure 143. *Metrosideros robusta* with epiphytes. Photo by Phil Bendle, through Creative Commons.

Wolf (1993d) used **relevés** (visual descriptions of vegetation of area plus habit and habitat data) to study epiphytes in the tropical montane rainforest in the northern Andes (Figure 31). This usually involves examining all the microhabitats and niches to find all possible species. They used rope-climbing techniques to reach the bryophytes.



Figure 144. *Metrosideros robusta* showing inner branches. Photo by Phil Bendle, through Creative Commons.

Rope Climbing

Early tropical researchers, in an attempt to get better representation of the canopy bryophytes, frequently used ropes to help them climb the trees (Wolf 1993a, b, c, 1995; Gradstein *et al.* 1996; Nadkarni 2000).

Sillett (1991) set out to develop a quantitative method for sampling tropical canopy bryophytes. He used hemispherical canopy photography to learn that interior crowns of isolated trees (Figure 145) are twice as bright as the interior crowns of intact forest trees of the same species (*Ficus tuerckheimii*; Figure 146). He climbed the trees to sample them. Sillett used a cost-benefit analysis that indicated more branches per tree and fewer plots per branch minimizes time but provides similar information.



Figure 145. Tree climbing on tropical montane isolated tree, showing the brightness of the canopy. Photo by F. Werner, courtesy of Robbert Gradstein.

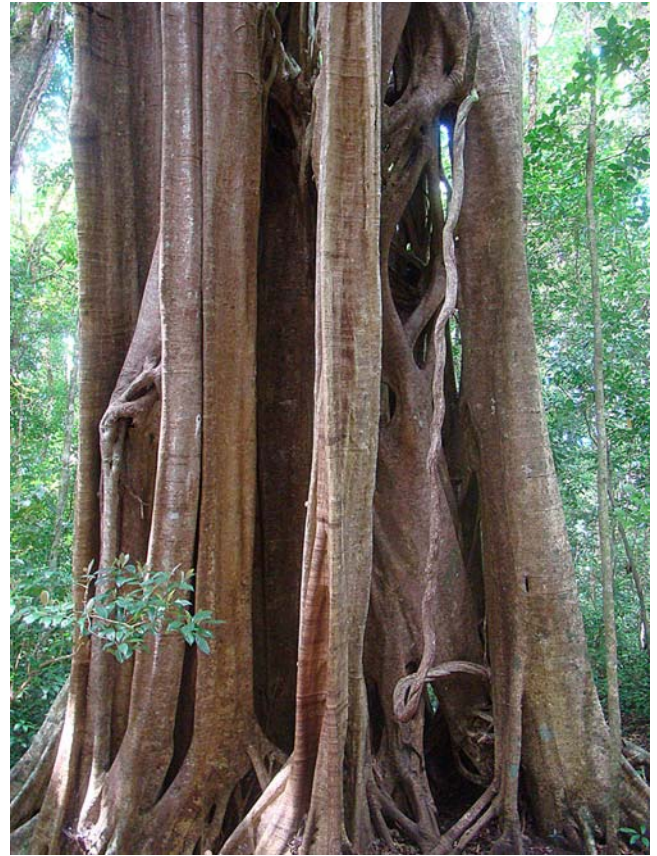


Figure 146. *Ficus tuerckheimii*, a species used by Sillett to develop methods for sampling the canopy. Photo by Dick Culbert, with online permission.

Older techniques such as tree climbing for collecting canopy bryophytes can present several problems. Many twigs and small branches cannot be reached from those branches that are strong enough to support the climber. Pole-climbing techniques require using a harness and the climbing spikes used can dislodge bryophytes and other epiphytes and put holes in the tree trunks, providing entry sites for pathogenic fungi and insects (Perry 1978). Inspired by Perry (1978), Cornelissen and ter Steege (1989) developed a rope-climbing technique that has been used by many researchers, including Dimitri Montfoort, Renske Ek, Jan Wolf, Ingo Holz, Nicole Nöske, Simone Sporn, Sylvia Mota de Oliveira, Laura Campos, and Angel Benitez, among others.

Using this method, Lücking *et al.* (1996) and Gradstein *et al.* (1996) reported that trees can be prepared for rope climbing in an hour, permitting the researcher to climb to 30 m in 5-10 minutes. Unfortunately, the outer branches are too fragile for climbing and must be sawed off.

Non-bryologists who collect may be fascinated by the epiphyllous species and usually do not provide representative sampling of the branch species. They furthermore often fail to provide the necessary data, such as substrate, that helps the taxonomist to identify the samples. While their collections are valuable to increase our knowledge of the species in an area, they can miss whole groups of taxa and should be used with caution for quantitative conclusions or ecological inferences.

Bow and Arrow

Perry (1978) modified the pole climbing techniques by adding ropes to the equipment. Once the rope is thrown over a sturdy branch, it can be used to help hoist the climber to the level of the branches. The placement of the rope is facilitated by use of an 80-pound pull crossbow and weighted arrow tied to 30-pound test monofilament. The weight of the arrow insures that the arrow will fall to the ground. A spool can be wrapped around the line to prevent tangling.

This is only the first step. Next, a 120-240 pound test braided line is attached to the first, smaller line (Perry 1978). The line that can support the climber is too heavy for the bow and arrow. The heavier (240 pound test) line is needed if there are many large branches because abrasion by the branches can break the lighter-weight line. Safety is a foremost concern.

Ter Steege and Cornelissen (1988) described rope climbing techniques (Figure 147-Figure 150) to climb trees to capture epiphytic bryophytes. These were based on previous use by Day (1962), Pike *et al.* (1975), Perry (1978), Perry and Williams (1981), Whitacre (1981), Hoi (1984). Ter Steege and Cornelissen (1986) used a rope technique in Guyana (Figure 93), Wolf (1986) in Colombia, Montfoort & Ek (1990) in French Guiana (Figure 140).

Ter Steege and Cornelissen (1988) emphasized safety aspects: making sure the branch is strong enough and has an angle of less than 45°; using a proper, strong knot; avoiding branches infected by parasites and hemiparasites. The technique requires shooting an arrow over the selected branch (Figure 147), carrying with it a strong nylon fishing line (50-60/100). Tangles are prevented by keeping the line on a fishing reel, preferably a sea-fishing reel, attached to the bow. The arrow head is weighted with lead to help it return to the ground through the branches. The arrow is then removed and a 3-mm cord is tied to the fishing line using a double sheet bend knot (Figure 147). Winding the reel helps to pull the line and attached cord over the branch. An 11-mm speleocord is attached to the 3-mm cord using a double sheet bend knot (see Figure 147 for knots). This 11-mm cord is hauled over the limb by hand power. Construct a lasso with a figure of eight knot and pull it against the limb. The 3-mm cord is attached to the free end of the knot to facilitate pulling the knot down after use. Test the strength of the branch by having **two** people hang onto it with their full weight. Be prepared to get out of the way if the branch breaks! Hang two ascenders or jumars (Figure 148) on the rope to facilitate ascent. Attach one ascender to a seat belt and the other to the climber's feet (Figure 148). Always use locking karabiners to link the ascenders (Figure 149-Figure 150). Another rope can be tossed over desired branches higher up, using a load attached to a 3-mm cord. The procedure of hanging a rope is then repeated. I recommend reading the original article for details. And if this vocabulary is unfamiliar to you, you might not have enough experience to use this method safely.

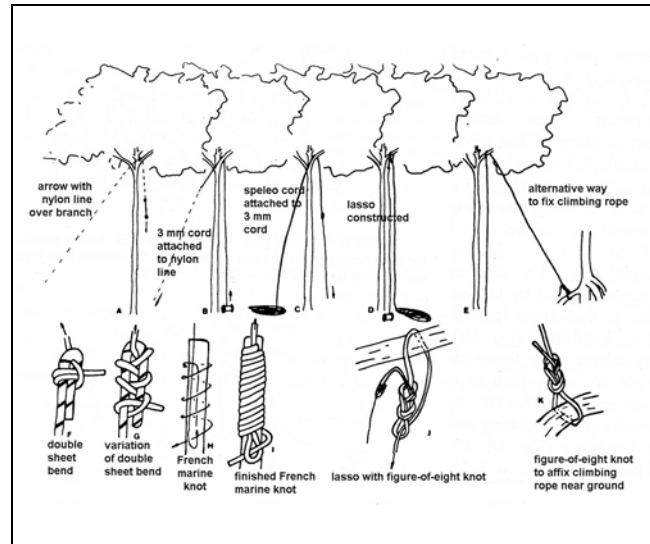


Figure 147. Knots used for rope climbing of trees. Modified from ter Steege & Cornelissen 1988.

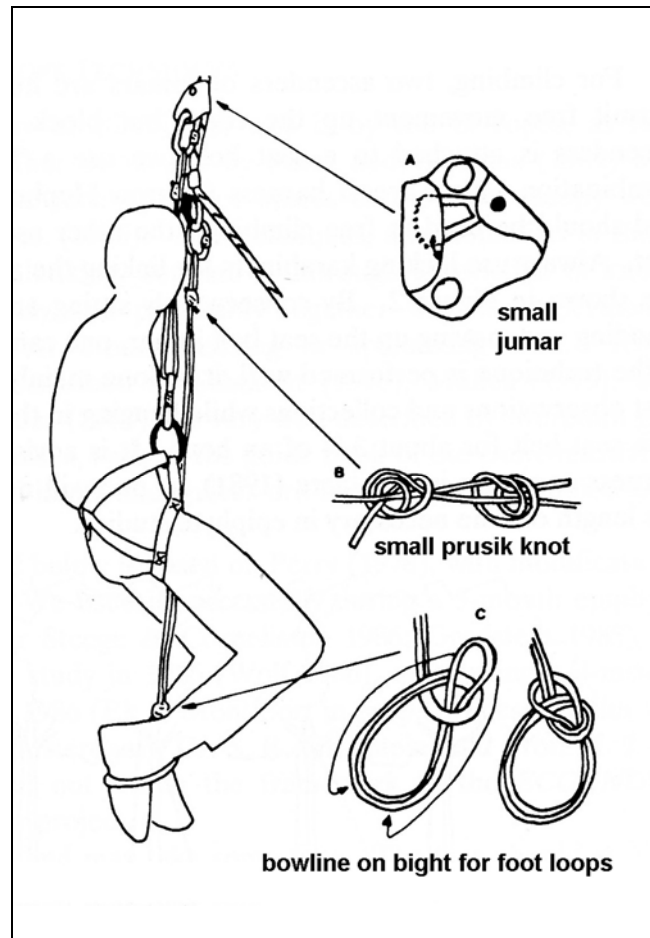


Figure 148. Climbing gear. Modified from ter Steege & Cornelissen 1988.

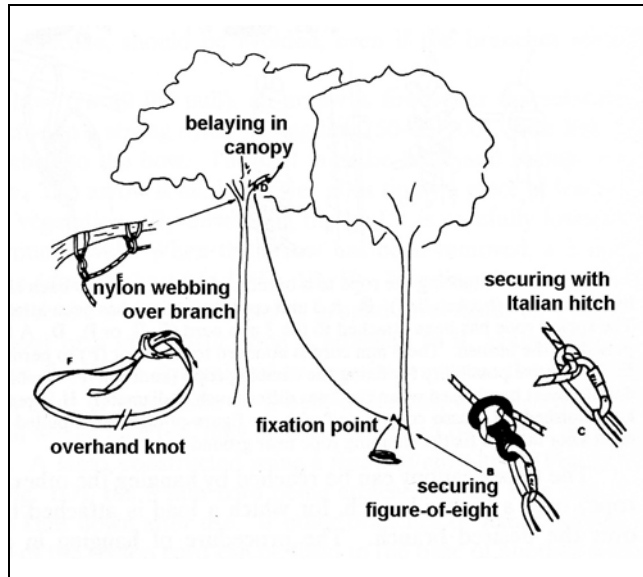


Figure 149. Free-climbing technique. Modified from ter Steege & Cornelissen 1988.



Figure 151. Canopy crane at Surumoni, Venezuela. Photo courtesy of Robbert Gradstein.

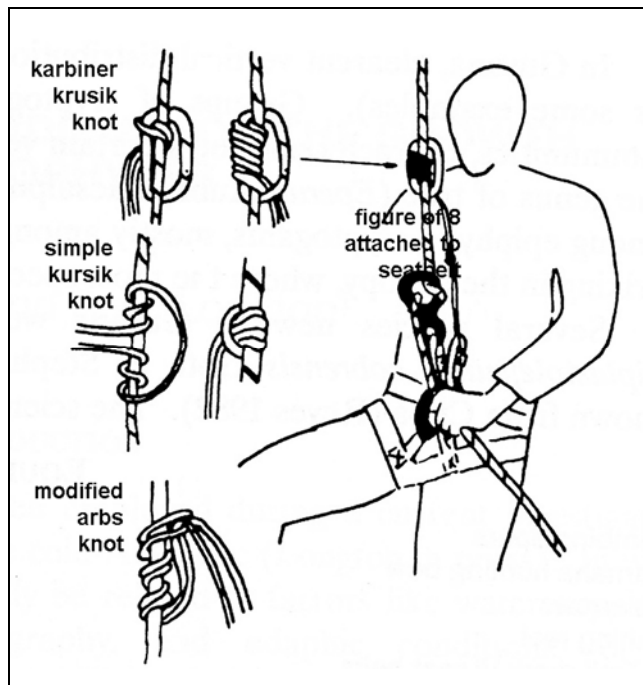


Figure 150. Rappelling knots. Modified from ter Steege & Cornelissen 1988.

Other Canopy Access

Hallé (1990) used an inflatable raft carried by a hot-air dirigible to gain access to canopy epiphytes. Other methods include the use of cranes (Figure 151-Figure 152) (Parker *et al.* 1992; Zotz & Vollrath 2003) and special platforms and walkways (Figure 153) (McClure 1966; Grison 1978; Perry 1978). Lowman *et al.* (2012) provide the standard modern reference on canopy research methods.



Figure 152. Canopy crane with gondola in Panama. Photo courtesy of Robbert Gradstein.



Figure 153. Costa Rica skywalk. Photo by Dirk van der Made, through Creative Commons.

Role

Gotsch *et al.* (2016) emphasized the importance of epiphytic material in tropical montane cloud forests (Figure 153). As noted earlier, they intercept both nutrients and moisture from the atmosphere and contribute these over an extended period of time to the forest floor. The amounts of these contributions vary with stand age and microclimate. This epiphytic biomass provides food sources for both birds and mammals, and birds use bryophytic biomass for nest building. Gotsch and coworkers state that more than 200 species of birds use the epiphytes. Wilding *et al.* (2016) cited a number of pendent genera of mosses and liverworts that are used in nest building. These included the mosses *Papillaria*, *Floribundaria*, *Meteorium*, and *Squamidium* and the liverworts *Frullania* and *Plagiochila*.

Barkman (1958) and Pócs (1980) suggested that bryophytes may cause their own displacement by retaining water that makes tracheophytic epiphyte presence possible. They furthermore form humus, accelerate bark decay (Barkman 1958), and facilitate anchorage of seeds and other propagules.

Adventitious Roots

Herwitz (1991) found that adventitious roots of the montane tropical rainforest canopy tree species *Ceratopetalum virchowii* (see Figure 154) take advantage of the nutrient-rich stemflow, whereas the stemflow of other canopy tree species is nutrient-poor. Such observations as this raise the question of the role of bryophytes in the development of adventitious roots.



Figure 154. *Ceratopetalum apetalum*; *Ceratopetalum virchowii* is a canopy tree in the tropical montane rainforest and uses adventitious roots to gain nutrients from stemflow. Photo by John Tann, through Creative Commons.

Nadkarni (1994) found that epiphytic bryophytes do provide a rooting medium for adventitious roots of trees. In fact, a dynamic interaction may occur in which the bryophytes help the tree, and the tree roots likewise help the establishment of the epiphytic community. The bryophyte mat traps inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson *et al.* 1992) that are leached from members of the epiphyte community. These nutrients nourish the roots of the tree (Nadkarni & Primack 1989). The two appear to grow in mutual benefit, with the roots benefitting from the nutrients and providing a larger anchoring system for the epiphytes as they grow (Nadkarni 1994). As the bryophytes and organic matter increase, they provide more leachates, causing the tree roots to increase.

Leary *et al.* (2004) found that nodulation of the legume *Acacia koa* (Figure 155) occurred in the canopy in Hawaii. These nodules contain the bacterium *Bradyrhizobium* (Figure 156) in pockets within the canopy. These pockets provide organic soils with trapped nutrients and often form among bryophytes. They even have lower aluminum levels than the terrestrial soils.



Figure 155. *Acacia koa*, Maui, Hawaii, a species that forms nodules in epiphytic organic soils, including among bryophytes. Photo by Forest and Kim Starr, through Creative Commons.

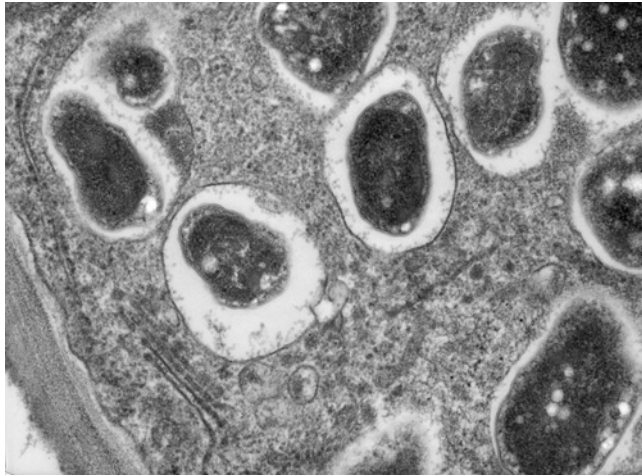


Figure 156. *Bradyrhizobium japonicum* from soybean root nodule. A species of *Bradyrhizobium* occurs in nodules among mosses on *Acacia koa*. Photo by Louisa Howard, through public domain.

Substrata for Tracheophytes

Zotz and Vollrath (2003) used a canopy crane (Figure 151-Figure 152) to explore the epiphyte flora of the palm *Socratea exorrhiza* (Figure 35-Figure 36) in a primary lowland rainforest of Panama. They examined each palm in a 0.9 hectare and identified 701 tracheophyte epiphytes and hemi-epiphytes on 118 palm trees, identifying 66 species. The tracheophytes usually do not colonize trees less than 20 years old. These tracheophytic epiphytes are significantly associated with bryophytes, but the researchers could find no species that seemed to depend on the bryophytes. On the other hand, one must wonder if the bryophytes are important in maintaining moisture for the roots and storing nutrients trapped during precipitation events, as well as providing a suitable anchor for germinating seeds.

In Madagascar, orchids commonly grow in beds of *Leucoloma* (Figure 157) on tree trunks (Pócs 1982; Catherine La Farge, Bryonet September 2004). The bryophytes trap nutrients that make them a suitable substrate for epiphytes.



Figure 157. *Leucoloma* sp, India, common substrate for orchids on tree trunks. Photo by Shyamal L., through Creative Commons.

But finding orchids among bryophytes does not indicate any necessary role for the bryophytes. Tremblay (2008) relocated a rare epiphytic orchid after its dislocation from Hurricane Georges. He found that the orchid population size did not correlate with the percent of moss cover on the standing trees. Nevertheless, the orchids seemed to be more frequent when the tree bole had 40-90% moss cover. We need studies to determine the role in bryophytes in trapping and holding seeds and seedlings until the orchids and other plants are able to attach to the tree.

Probably the best example of a moss-dwelling epiphyte is the neotropical fern genus *Melpomene* (Figure 158). Almost all species in this genus grow in dense epiphytic bryophyte mats (Lehnert 2007). Sylvester *et al.* (2014) noted that the highest epiphyte elevation known for a tracheophyte was from the southern Peruvian Andes. They reported three species of the fern *Melpomene* from *Polylepis pepeii* (see Figure 159) forests above 4,250 m, with *Melpomene peruviana* reaching close to 4,550 m asl. Could it be that bryophytes contribute in some way to their ability to live at these high elevations?



Figure 158. *Melpomene firma* and *M. monoliformis* – grammitid ferns, both species that grow in dense bryophyte mats in trees. Photo by Marcus Lehnert, courtesy of Robert Gradstein.



Figure 159. *Polylepis rugulosa* in the Andes; *Polylepis pepeii* is host to *Melpomene* species in the Andes. Photo by Alexander Yates, through Creative Commons.

Ferns often inhabit bryophyte mats, where the bryophytes may support the heavy weight of the rhizome on vertical surfaces. Kelly *et al.* (2004) reported that *Elaphoglossum hoffmannii* was typically associated with mosses, specifically with *Syrrhopodon gaudichaudii* (Figure 160). *Elaphioglossum wawrae* (Figure 161) is a Hawaiian epiphytic endemic that occurs in moss mats, and is among the tracheophyte species that characterize the montane zone (Higashino *et al.* 1988; Kitayama and Mueller-Dombois 1992). *Elaphoglossum glabellum* growing on *Epeura falcata* (Figure 42-Figure 43) is restricted to small moss mats that occur around forks and knots found only in the lower canopy in the lowland rainforest of Guyana (Figure 93) (ter Steege & Cornelissen 1989). On *Epeura grandiflora*, this species occurs on bryophyte mats from the lower trunk to the middle canopy. The bryophyte mats provide a longer supply of water. But bark differences may account for the differences in bryophyte cover, with *E. grandiflora* having rougher bark than that of *E. falcata*. They may also provide a chemical buffer against toxins in the bark (Frei 1973).



Figure 160. *Syrrhopodon gaudichaudii*, a species that typically is found with *Elaphoglossum hoffmannii*. Photo by Michael Lüth, with permission.



Figure 161. *Elaphoglossum wawrae* among mosses, a fern endemic to Hawaii that seems to benefit from an association with bryophytes. Photo from USDA, through public domain.

On the other hand, Werner and Gradstein (2008) studied the factors important for seedling establishment of tracheophytic epiphytes in the Andes and found no relationship to bryophyte cover. Rather, isolated trees closer to the forest had significantly greater colonization by these plants, but colonization did not correlate with greater canopy or bryophyte cover.

Friend or Foe?

Cacao plantation owners had concerns over the epiphytes on the leaves, removing them in an effort to improve productivity of the fruit crop (Sporn *et al.* 2007). Removal of epiphytes from cacao had no notable effect on the harvest size of the cacao trees.

But sometimes the bryophytes seem to have negative effects on these trees. Akinfenwa (1989) reported that the epiphytic moss *Erythrodontium barteri* (Figure 162) reduced yield of the *Theobroma cacao* (Figure 163) trees. They cause a "dressing" effect on palms wherein the leaf bases collect soil in the leaf axils. This soil supports an epiphytic community with microbial activities in the soil. The result is decay of leaf bases, causing the joints to weaken. They can no longer support the epiphytic community, causing it to fall gradually along with the remains of the leaf bases. This process continues as the trees age and grow taller, resulting in smooth boles and consequently fewer leaves for photosynthesis.



Figure 162. *Erythrodontium squarrosus* from the Neotropics; *E. barteri* is known to reduce yield in the cocoa tree, *Theobroma cacao*. Photo by Michael Lüth, with permission.

Faunal Habitat

The epiphytes provide a suitable habitat for a number of arthropods in the Neotropical cloud forest (Yanoviak *et al.* 2004). The arthropod morphospecies are similar between green and brown portions of the epiphyte mats, but relative abundances often differ. The most common of these arthropods was an oribatid mite; these preferred the brown portion in laboratory trials.

Bryophytes are home to a variety of frogs and salamanders and are even used by chimpanzees to gather water. Birds use them for nesting material. These interesting interactions are discussed in the volume on Interactions.



Figure 163. *Theobroma cacao* in the Dominican Republic, host of epiphytic bryophytes. Photo by C. T. Cooper, through public domain.

Summary

Bryophytes exhibit a number of adaptations to the epiphyte living style. Many of these relate to the usually dry habitat and short duration of available water. The adaptations include green, multicellular spores, sexual dimorphism, asexual reproduction, monoicous condition, rhizoid discs, hyaline leaf margins, and cushion life forms. Their life strategies are typically **perennial stayers** and **perennial shuttle species**. In humid lowland areas **mats** are typical, contrasting with the **fans** and **wefts** that rely on propagules and clonal growth in the montane rainforest. Ciliate leaves collect water. In the xeric open, upper montane forests, **short turfs**, **tall turfs**, and **cushions** predominate. The understory often has **dendroids** and fans while the crowns have more **tufts**. In other cases, the inner branches have **tall turfs** and the outer ones have **smooth mats**. **Fans** and **mats** predominate in floodplains. **Colonists** occur almost exclusively in secondary forests.

The large spores facilitate short-distance dispersal and rapid development when water is available. Arrival on the tree bark appears to be a random event. Succession begins with crustose and foliose lichens and typically proceeds from the underside of the branch upward, although some observers conclude that the lichens inhibit the bryophytes. Ants may sometimes help in the dispersal. Rough bark is more easily colonized and holds more water for growth.

Host specificity is less important than tree characteristics. These relate to bark characteristics, leeward vs windward exposure, height on tree, tree size, and degree of uprightness. The inner canopy has thick branches and fewer bryophyte taxa compared to the thinner middle canopy branches, with greatest richness in the outer canopy. Many species are **facultative** epiphytes. Increasing bark pH seems to result in decreased bryophyte richness. Tree base, trunk, and crown differ due to light, moisture, and nutrients. Approximately 45-50% of the species occur in the crowns of rainforest trees.

Tropical forests have an array of vertical niches, but on a horizontal scale, 4-5 trees are adequate to find 95% of the diversity. The **Lejeuneaceae** are common in the canopy as branch epiphytes and as epiphylls. Tree bases often have **mats** and **wefts** of *Thuidium* spp., with *Fissidens* spp., **Lejeuneaceae**, and **Orthotrichaceae**. Farther up the trunk are **feather** types. **Dendroids**, **feathers**, and **brackets** occur on narrow stems of small trees and branches of shrubs in the understory. Species on the upper trunk are more appressed and correlate with structure of the phorophyte stands and to temperature zones. The lower branches and thick canopy branches typically have large **mats**; epiphyllous **Lejeuneaceae** abound. In moist forests, twigs support **pendent Meteoriaceae**, **Pterobryaceae**, *Frullania*, and **Lejeuneaceae**. On drier twigs one can find **Cryphaeaceae**, **Erpodiaceae**, **Orthotrichaceae**, **Sematophyllaceae**, *Frullania*, and **Lejeuneaceae**. The outer canopy contrasts with the inner canopy by having more light and less moisture, creating a stressful environment.

Logs and decaying wood are the primary substrate on the forest floor, raised above the thick litter layer. Dominant bryophytes are in the **Sematophyllaceae**, **Hookeriaceae**, and **Leucobryaceae**. Under stable climatic conditions, **perennial stayers** precede **wefts** and **mat**, a succession similar to that of the trunk epiphytic communities. Flood disturbance favors **dendroid** and **mat-forming shuttle species** that utilize a diaspore bank. In dry conditions, species are more likely to be **short-turf-forming** colonists. Shady sites are most suitable for **wefts**.

Epiphyte sampling is best done with ropes or bow and arrow, unless cranes or skywalks are available, minimizing damage to the trees and their flora. Quadrats in all tree zones can permit quantitative sampling. **Life forms** are suitable for assessing functional ecology.

Bryophyte clumps can provide moist rooting media for adventitious roots, and rooting media for ferns and orchids. They retain water, and store nutrients that can be released in pulses. Numerous invertebrate and amphibian species live among them.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about.

Literature Cited

- Affeld, K., Sullivan, J., Worner, S. P., and Didham, R. K. 2008. Can spatial variation in epiphyte diversity and community structure be predicted from sampling vascular epiphytes alone. *J. Biogeogr.* 35: 2274-2288.
- Akinfenwa, F. 1989. Occurrence of epiphytes on cocoa: A Survey. A paper presented at the 3rd Annual conference of Botanical Society of Nigeria held 5-9 March, 1989 at the University of Lagos, Nigeria.

- Andersohn, C. 2004. Does tree height determine epiphyte diversity? *Selbyana* 25: 101-117.
- Barkman, J. J. 1958. *Phytosociology and Ecology of Cryptogamic Epiphytes*. Van Gorcum & Co., Assen, Netherlands, 628 pp.
- Batista, W. V. S. and Santos, N. D. dos. 2016. Can regional and local filters explain epiphytic bryophyte distributions in the Atlantic Forest of southeastern Brazil? *Acta Bot. Brasil.* 30: 462-472.
- Benavides, J. C., Idarraga, A., and Alvarez, E. 2004. Bryophyte diversity patterns in flooded and tierra firme forests in the Aracua Region, Colombian Amazonia. *Trop. Bryol.* 25: 117-126.
- Blüthgen, N., Schmit-Neuerburg, V., Engwald, S., and Barthlott, W. 2001. Ants as epiphyte gardeners: Comparing the nutrient quality of ant and termite canopy substrates in a Venezuelan lowland rain forest. *J. Trop. Ecol.* 17: 887-894.
- Bryant, E. H., Crandall-Stotler, B., and Stotler, R. E. 1973. A factor analysis of the distribution of some Puerto Rican liverworts. *Can. J. Bot.* 51: 1545-1554.
- Cornelissen, J. H. C. and Gradstein, S. R. 1990. On the occurrence of bryophytes and macrolichens in different lowland rain forest types at Mabura Hill, Guyana. *Trop. Bryol.* 3: 29-35.
- Cornelissen, J. H. C. and Karssemeijer, G. J. 1987. Bryophyte vegetation on spruce stumps in the Hautes-Fagnes, Belgium, with special reference to wood decay. *Phytocoenologia* 15: 485-504.
- Cornelissen, J. H. C. and Steege, H. ter. 1986. Vertical distribution of epiphytes in a rainforest of Guiana. *Flora Guianensis* 3: 17-19.
- Cornelissen, H. and Steege, H. ter. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.
- Coxson, D. S., McIntyre, D. D., and Vogel, H. J. 1992. Pulse release of sugars and polyols from canopy bryophytes in tropical montane rain forest (Guadeloupe, French West Indies). *Biotropica* 24(2a): 121-133.
- Day, C. L. 1962. *Knots and splices*. Adlard Coles Ltd., London, pp. 1-74.
- Delia, R., Búcaro, R., Touw, A., and Stech, M. 2015. Epiphytic mosses from the understory of a forest in El Zancudo ("Los Bolsones"), La Paz, Honduras. *Bryo. Div. Evol.* 36: 45-50.
- Dengke, L. and Wu, P. 1988. A study of the epiphyllous liverworts of China (4) – The epiphyllous liverworts of Jinggang Shan, Jiangxi Province. *Invest. Stud. Nat. (Mus. Hist. Nat. Shanghai)* 1988(8): 38-42.
- DeVries, P. 1988. The use of epiphylls as larval hostplants by the tropical rionid butterfly, *Sarota gyas*. *J. Nat. Hist.* 22: 1447-1450.
- Dial, R. and Tobin, S. C. 1994. Description of arborist methods for forest canopy access and movement. *Selbyana* 15(2): 24-37.
- During, H. J. 1979. Life strategies of bryophytes: A preliminary review. *Lindbergia* 5: 2-18.
- Egunyomi, A. 1975. Studies of the biology and ecology of *Octoblepharum albidum*. Ph.D. thesis, University of Ibadan.
- Egunyomi, A. 1978. The distribution of the pantropic moss *Octoblepharum albidum*. Hedw. in Africa with special reference to Nigeria. *Rev. Bryol. Lichénol.* 44: 141-148.
- Egunyomi, A. and Olarinmoye, S. O. 1983. Studies on the distribution and vegetative reproduction of *Calymperes palisotii* Schwaegr. *Zeitschrift für Kryptogamenkunde*. Nova Hedw. 38: 487-499.
- Equihua, C. and Equihua, M. 2007. Spatial distribution of *Bryopteris filicina* on tree trunks of the Selva Lacandona, Chiapas, Mexico. *Bryologist* 110: 766-775.
- Ezukanma, I. O., Tessler, M., Salaam, A. M., Chukwuka, K. S., and Ogunniran, A. J. 2019. Epiphytic bryophytes of urban agroforests in Ibadan, Southwest, Nigeria. *J. Bryol.* (in press).
- Ford, L. 1994. The vertical distribution of epiphytes on *Sloanea woollsii* in Gambul State Forest southeast Queensland. *Australasian Bryol. Newslett.* 31: 6.
- Frahm, J.-P. 1990. The ecology of epiphytic bryophytes on Mt. Kinabalu, Sabah (Malaysia). *Nova Hedw.* 51: 121-132.
- Frahm, J.-P. 2003. *Manual of Tropical Bryology*. *Trop. Bryol.* 23: 1-196.
- Frahm, J.-P. and Kürschner, H. 1989. Was Moose auf die Bäume treibt. [What drives mosses on the trees.]. *Forschung* 4: 18-22.
- Frahm, J.-P., Specht, A., Reifenrath, K., and Vargas, Y. L. 2000. Allelopathic effect of crustaceous lichens on epiphytic bryophytes and vascular plants. *Nova Hedw.* 70: 245-254.
- Frei, S. J. K. 1973. Orchid ecology in a cloud forest in the mountains of Oaxaca, Mexico. *Amer. Orchid Soc. Bull.* 42: 307-314.
- Freiberg, M. and Freiberg, E. 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. *J. Trop. Ecol.* 5: 673-688.
- Frey, W. and Kürschner, H. 1991. Lebensstrategien epiphytischer Bryophyten im tropischen Tieflandsund Bergregenwald am Mt. Kinabalu (Sabah, Northern Borneo). [Life strategies of epiphytic bryophytes in tropical lowland and mountain rainforest on Mt. Kinabalu (Sabah, Northern Borneo).]. *Nova Hedw.* 53: 307-330.
- Frey, W., Goßow, R., and Kürschner, H. 1990. Verteilungsmuster von Lebensformen, wasserlentenden und wassspeichernden Strukturen in epiphytischen Moosgesellschaften am Mt. Kinabalu (NordBorneo). [Distribution patterns of life forms, water-leaching and water-storing structures in epiphytic moss communities on Mt. Kinabalu (North Borneo).]. *Nova Hedw.* 51: 87-119.
- Frey, W., Kürschner, H., and Seifert, U. H. 1995. Scientific Results of the BRYOTROP expedition to Zaire and Rwanda. 7. Life strategies of epiphytic bryophytes from tropical lowland and montane forests, ericaceous woodlands and the *Dendrosenecio subparamo* of the eastern Congo basin and adjacent mountains (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). *Trop. Bryol.* 11: 129-150.
- Gehrig-Downie C., Obregón A., Bendix J., and Gradstein S. R. 2013. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *J. Bryol.* 35: 243-254.
- Germano, S. R. and Pôrto, K. C. 1996. Floristic survey of epixylic bryophytes of an area remnant of the Atlantic forest (Timbauba – PE, Brazil). 1. Hepaticopsida (except Lejeuneaceae) and Bryopsida. *Trop. Bryol.* 12: 21-28.
- Germano, S. R. and Pôrto, K. C. 1997. Ecological analysis of epixylic bryophytes in relation to the decomposition of substrate (Municipality of Timbauba-Pernambuco, Brazil). *Cryptog. Bryol. Lichénol.* 18: 143-150.
- González-Mancebo, J. M., Losada-Lima, A., and McAlister, S. 2003. Host specificity of epiphytic bryophyte communities in a laurel forest on Tenerife (Canary Islands, Spain). *Bryologist* 106: 383-394.
- Gotsch, S. G., Nadkarni, N., and Amici, A. 2016. The functional roles of epiphytes and arboreal soils in tropical montane cloud forests. *J. Trop. Ecol.* 32: 455-468.

- Gradstein, S. R. 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. *Cryptog. Bryol.* 27(1): 141-152.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies.* Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R. and Sporn, S. G. 2010. Diversity of epiphytic bryophytes along land use gradients in the tropics. *Nova Hedw. Beih.* 138: 309-321.
- Gradstein, S. R., Hietz, P., Lücking, R., Lücking, A., Sipman, H. J. M., Vester, H. F. M., Wolf, J. H. D., and Gardette, E. 1996. How to sample the epiphytic diversity of tropical rain forests. *Ecotropica* 2: 59-72.
- Gradstein, S. R., Griffin, D. III, Morales, M. I., and Nadkarni, N. M. 2001. Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia* 23: 203-212.
- Gradstein, S. R., Nadkarni, N. M., Krömer, T., Holz, I., and Nöske, N. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. *Selbyana* 24: 105-111.
- Grison, F. 1978. Amélioration genetique de L'Okoume. *Bois et Forets de Tropiques* 179: 3-26.
- Hallé, F. 1990. A raft atop the rain forest. *Natl. Geogr.* 178: 128-138.
- Herwitz, S. R. 1991. Aboveground adventitious roots and stemflow chemistry of *Ceratopetalum virchowii* in an Australian montane tropical rain forest. *Biotropica* 23: 210-218.
- Hietz, P. 1997. Population dynamics of epiphytes in a Mexican humid montane forest. *J. Ecol.* 85: 767-775.
- Higashino, P. K., Cuddihy, L. W., Anderson, S. J., and Stone, C. P. 1988. Checklist of vascular plants of Hawaii Volcanoes National Park. Technical Report 64. Cooperative National Park Resources Studies Unit, University of Hawaii at Manoa.
- Hoi, K. 1984. Seiltechnik. Teufelberger, Wels, pp. 1-35.
- Holz, I., Gradstein, S. R., Heinrichs, J., and Kappelle, M. 2002. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. *Bryologist* 105: 334-348.
- Iwatsuki, Z. 1960. The epiphytic bryophyte communities in Japan. *J. Hattori Bot. Lab.* 22: 160-352.
- Jaag, O. 1943. Untersuchungen über den Rhythmus der Lauberneuerung, die Lebensdauer der Blätter und den Epiphytenbefall bei einigen Farnen in den Tropen. [Studies on the foliage renewal rate, leaf life and epiphyte involvement in some ferns in the tropics.]. *Mitt. Naturf. Ges. Schaffhausen.*
- Jarman, S. J. and Kantvilas, G. 1995. Epiphytes on an old Huon pine tree (*Lagarostrobos franklinii*) in Tasmanian rainforest. *N. Z. J. Bot.* 33: 65-78.
- Johansson, D. 1974. Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr. Suecica* 59: 1-136.
- Jovet-Ast, S. 1953. Le genre *Colura*. *Rev. Bryol. Lichénol.* 22: 206-312.
- Kelly, D. L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S. O., and Marciano-Berti, L. 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: Patterns in the distribution of the flora. *J. Trop. Ecol.* 20: 643-666.
- Kitayama, K. and Mueller-Dombois, D. 1992. Vegetation of the wet windward slope of Haleakala, Maui, Hawaii. *Pacific Sci.* 46: 197-220.
- Krömer, T., Kessler, M., and Gradstein, S. R. 2007. Vertical stratification of vascular epiphytes in submontane and montane forests of the Bolivian Andes: The importance of the understory. *Plant Ecol.* 189: 261-278.
- Kruijt, B., Malhi, Y., Lloyd, J., Norbre, A. D., Miranda, A.C., Pereira, M. G. P., Culf, A., and Grace, J. 2000. Turbulence statistics above and within two Amazon rain forest canopies. *Boundary-Layer Meteorol.* 94: 297-331.
- Kürschner, H. 1990. Höhengliederung (ordination) von epiphytischen Laubund Lebermoosen in Nord-Borneo (Mt. Kinabalu). [Height classification (ordination) of epiphytic hardwood liverworts in northern Borneo (Mt. Kinabalu).]. *Nova Hedw.* 51: 77-86.
- Kürschner, H. 2000. Epiphytische Moosgemeinschaften tropischer Regenwälder-Adaptionen und floristisch-historische Entwicklung. [Epiphytic moss communities of tropical rainforest – Adaptations and floristic-historical development.]. *Berichte der Reinhold-Tüxen-Gesellschaft* 12: 187-206.
- Kürschner, H. 2003. Epiphytic bryophyte communities of southwestern Arabia – phytosociology, ecology and life strategies. *Nova Hedw.* 77: 55-71.
- Kürschner, H. 2004a. Life strategies and adaptations in bryophytes from the Near and Middle East. *Turkish J. Bot.* 28: 73-84.
- Kürschner, H. 2004b. Phytosociology, ecology and life strategies of a remarkable epiphytic bryophyte community of Socotra Island, Yemen. *Bot. Jahrb. Syst.* 125: 377-395.
- Kürschner, H. and Parolly, G. 1998a. Lebensstrategien stammepiphytischer moose in regenwaldern am andenostabhang und im Amazonas-Tiefland von nord-Peru. [Life strategies of epiphytic bryophyte vegetation in rainforests along the eastern Andean slopes and the Amazon lowlands of northern Peru]. *Nova Hedw.* 67: 1-22.
- Kürschner, H. and Parolly, G. 1998b. Lebensformen und Adaptationen zur Wasserleitung und Wasserspeicherung in epiphytischen Moosgesellschaften Nord-Perus (Amazonas-Tiefland, Cordillera Oriental, Cordillera central). [Life forms and adaptations to water conduction and water storing in epiphytic bryophyte communities in northern Peru (the Amazon lowlands, eastern and central cordillera).]. *Nova Hedw.* 67: 349-379.
- Kürschner, H. and Parolly, G. 1998c. Syntaxonomy of trunk-epiphytic bryophyte communities of tropical rain forests: A first pantropical approach. *Phytocoenologia* 28: 357-425.
- Kürschner, H. and Parolly, G. 2005. Ecosociological studies in Ecuadorian bryophyte communities. III. Life forms, life strategies and ecomorphology of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedw.* 80: 89-113.
- Kürschner, H. and Parolly, G. 2007. Life forms and life strategies in tropical trunk-epiphytic bryophytes – a case study from Ecuador. *Beih. Nova Hedw.* 131: 121-131.
- Kürschner, H. and Seifert, U. H. 1995. Wissenschaftliche Ergebnisse der BRYOTROP-Expedition nach Zaire und Rwanda. 6. Lebensformen und Adaptationen zur Wasserleitung und Wasserspeicherung in epiphytischen Moosgesellschaften im östlichen Kongobecken und den angrenzenden Gebirgsstöcken (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/ Rwanda). [Scientific results of the BRYOTROP expedition to Zaire and Rwanda. 6. Life forms and adaptations to the aqueduct and water storage in epiphytic moss communities in the eastern Congo basin and the adjacent mountain ranges (Parc National de Kahuzi-Biega / Zaire, Forêt de Nyungwe / Rwanda). *Trop. Bryol.* 11: 87-118.

- Kürschner, H., Tonguç, Ö., and Yayintas, A. 1998. Life strategies of epiphytic bryophyte communities of the southwest Anatolian *Liquidambar orientalis* forests. *Nova Hedw.* 66: 435-450.
- Kürschner, H., Frey, W., and Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – A pantropical synopsis. *Nova Hedw.* 69: 73-99.
- Kürschner, H., Parolly, G., and Erdag, A. 2006. Life forms and life strategies of epiphytic bryophytes in *Quercus vulcanica* forest of Turkey. *Nova Hedw.* 82: 331-347.
- Kürschner, H., Stech, M., Sim-Sim, M., Fontinha, S., and Frey, W. 2007. Life form and life strategy analyses of the epiphytic bryophyte communities of Madeira's laurel and ericaceous forests. *Bot. Jahrb. Syst. Pflanzen.* 127: 151-164.
- Laman, T. G. 1995. *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. *Ecology* 76: 2617-2626.
- Leary, J. J., Singleton, P. W., and Borthakur, D. 2004. Canopy nodulation of the endemic tree legume *Acacia koa* in the mesic forests of Hawaii. *Ecology* 85: 3151-3157.
- Lee, L. C., Liong, C.-Y., and Jemain, A. A. 2017. Q-mode versus R-mode principal component analysis for linear discriminant analysis (LDA). In: AIP Conference Proceedings, Vol. 1842, No. 1, p. 030024, AIP Publishing.
- Leerdam, A. van, Zagt, R. J., and Veneklaas, E. J. 1990. The distribution of epiphyte growth-forms in the canopy of a Colombian cloud-forest. *Vegetatio* 87: 59-71.
- Lehnert, M. 2007. Revision of *Melpomene*. Ph. D. Dissertation, University of Göttingen. Published 2013 as *Flora Neotropica Monograph* 112.
- Longino, J. T. and Nadkarni, N. M. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a Neotropical montane forest. *Psyche* 97: 81-94.
- Lovai, I., Cairns, A., and Congdon, R. A. 2012. A comparison of three protocols for sampling epiphytic bryophytes in tropical montane rainforest. *Trop. Bryol.* 34: 93-98.
- Lowman, M. D., Schowalter T., and Franklin, J. 2012. *Methods in Forest Canopy Research*, University of California Press, Oakland, 240 pp.
- Lücking, R., Lücking, A., Gradstein, S. R., Hietz, P., Lücking, R., Lücking, A., and Gardette, E. 1996. How to sample the epiphytic diversity of tropical rain forests. V. Follicolous bryophytes and lichens. *Ecotropica* 2: 67-72.
- Mägdefrau, K. 1982. Life-forms of bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Springer, Dordrecht, pp. 45-58.
- Mari, M. L. G., Toledo, J. J., Nascimento, H. E. M., and Zartman, C. E. 2016. Regional and fine scale variation of holoepiphyte community structure in central Amazonian white-sand forests. *Biotropica Special Issue: Neotropical White-Sand Forests*, pp. 70-80.
- Mattila, P. and Koponen, T. 1999. Diversity of the bryophyte flora and vegetation on rotten wood in rain and montane forests in northeastern Tanzania. *Trop. Bryol.* 16: 39-164.
- McClure, H. 1966. Flowering, fruiting and animals in the canopy of a tropical rainforest. *Malaysian Forester* 29: 182-203.
- Medeiros, A. C., Loope, L. L., and Anderson, S. J. 1993. Differential colonization of epiphytes on native (*Cibotium*) spp. and alien (*Cyathea cooperi*) tree ferns in a Hawaiian rain forest. *Selbyana* 14: 71-74.
- Montfoort, D. and Ek, R. C. 1990. Vertical distribution and ecology of epiphytic bryophytes in a lowland rain forest of French Guiana. Institute of Systematic Botany, University of Utrecht, Utrecht.
- Müller, U. G. and Frahm, J.-P. 1998. Diversität epiphytischer Moose eines westandinen Bergregenwaldes in Ecuador. [Diversity of epiphytic mosses of a Westand mountain rainforest in Ecuador.]. *Trop. Bryol.* 15: 29-44.
- Nadkarni, N. M. 1986. The effects of epiphytes on precipitation chemistry in a Neotropical cloud forest. *Selbyana* 9: 44-51.
- Nadkarni, N. M. 1994. Factors affecting the initiation and elongation of above-ground adventitious roots in a tropical cloud forest tree: An experimental approach. *Oecologia* 100: 94-97.
- Nadkarni, N. M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica* 32: 358-363.
- Nadkarni, N. M. and Primack, R. B. 1989. A comparison of mineral uptake and translocation by above-ground and below-ground root systems of *Salix syringiana*. *Plant Soil* 113: 39-45.
- Nadkarni, N. M., Cobb, A. R., and Solano, R. 2000. Interception and retention of macroscopic bryophyte fragments by branch substrates in a tropical cloud forest: An experimental and demographic approach. *Oecologia* 122: 60-65.
- Nehira, K. 1983. Spore germination, protonema development and sporophyte development. In: Schuster, R. M. (ed.). *New Manual of Bryology*, Vol. 1. Hattori Botanical Laboratory, Nichinan, Japan, pp. 343-385.
- Olarinmoye, S. O. 1977. Studies on the epiphyllous liverworts – phorophyte relationship. *Nova Hedw.* 27: 647-654.
- Olarinmoye, S. O. 1981. Reactions of *Radula flaccida* Lindenb. & Gott. to leaf leachates and extracts. *Misc. Bryol. Lichenol.* 9: 56-59.
- Olarinmoye, S. O. 1982. Reactions of *Radula flaccida* Lindenb. & Gottsche to leaf leachates and extracts. *Cryptog. Bryol. Lichénol.* 3: 7.
- Oliveira, S. M. 2010. Diversity of Epiphytic Bryophytes across the Amazon. Ph.D. Dissertation, Universiteit Utrecht. 152 pp.
- Oliveira, S. M. and Steege, H. ter. 2013. Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. *Acta Bot. Brasil.* 27: 347-363.
- Oliveira, S. M. and Steege, H. ter. 2015. Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *J. Ecol.* 103: 441-450.
- Oliveira, S. M., Steege, H. ter, Cornelissen, J. H., and Gradstein, S. R. 2009. Niche assembly of epiphytic bryophyte communities in the Guianas: A regional approach. *J. Biogeogr.* 36: 2076-2084.
- Oliveira, S. M., with Steege, H. ter, Cornelissen, J. H. C., and Gradstein, S. R. 2010. Niche assembly of epiphytic bryophyte communities in the Guianas: A regional approach. In: Oliveira, S. M. Diversity of Epiphytic Bryophytes across the Amazon. Ph.D. dissertation, Universiteit Utrecht, pp. 15-38.
- Pardow, A., Gehrig-Downie, C., Gradstein, R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. *Biodiv. Conserv.* 21: 3637-3655.
- Parker, G., Smith, A., and Hogan, K. 1992. Access to the upper forest canopy with a large tower crane. *BioScience* 42: 664-670.
- Parolly, G. and Kürschner, H. 2005. Ecosociological studies in Ecuadorian bryophyte communities. V. Syntaxonomy, life forms and life strategies of the bryophyte vegetation on

- decaying wood and tree bases in S Ecuador. *Nova Hedw.* 81: 1-35.
- Perry, D. R. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155-157.
- Perry, D. R. and Williams, J. 1981. The tropical rainforest canopy: A method providing total access. *Biotropica* 13: 282-285.
- Pike, L. H., Dennison, W. C., Tracy, D. M., Sherwood, M. A., and Rhoades, F. M. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in Western Oregon. *Bryologist* 78: 389-402.
- Pócs, T. 1974. Bioclimatic studies in the Uluguru Mts. *Acta Bot. Acad. Sci. Hung.* 20: 115-135.
- Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Acad. Sci. Hung.* 26: 143-167.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, London, pp. 59-104.
- Pócs, T. 1989. 28. A preliminary study of the undergrowth of primary and secondary submontane rainforests in the East Usambara Mountains, with notes on epiphytes. In: Hamilton, A. C. and Bensted-Smith, R. (eds.). *Forest Conservation in the East Usambaras*. IUCN – The World Conservation Union Forest Division, Ministry of Lands, Natural Resources and Tourism United Republic of Tanzania, pp. 301-306.
- Poore, M. E. D. 1955. The use of phytosociological methods in ecological investigations: I. The Braun-Blanquet System. *J. Ecol.* 43: 226-244.
- Proctor, M. C. F. 2004. Light and desiccation responses of *Weymouthia mollis* and *W. cochlearifolia*, two pendulous rainforest epiphytes from Australia and New Zealand. *J. Bryol.* 26: 167-173.
- Richards, P. W. 1954. Notes on the bryophyte communities of lowland tropical rain forest, with special reference to Moraballi Creek, British Guiana. *Vegetatio* 6: 319-328.
- Richards, P. W. 1984. The ecology of tropical forest bryophytes. In: Schuster, R. M. (ed.). *New Manual of Bryology*. Vol. 2. Hattori Botanical Laboratory, Nichinan, pp. 1233-1270.
- Romero, C. 1999. Reduced-impact logging effects on commercial non-vascular pendant epiphyte biomass in a tropical montane forest in Costa Rica. *Forest Ecol. Mgmt.* 118: 117-125.
- Rudolph, D., Rauer, G., Nieder, J., and Barthlott, W. 1998. Distributional patterns of epiphytes in the canopy and phorophyte characteristics in a western Andean rain forest in Ecuador. *Selbyana* 19: 27-33.
- Santos, E. L. D., Oliveira, H. C., and Peralta, D. F. 2018. Floristic composition and vertical zonation of epiphytic bryophytes in Dense Montane Ombrophilous Forest in southern Brazil. *Bryologist* 121: 547-553.
- Sastre-de Jesús, I. 1992. Estudios preliminares sobre comunidades de briofitas en troncos en descomposición en el bosque subtropical lluvioso Puerto Rico. *Trop. Bryol.* 6: 181-192.
- Schofield, W. B. 1985. *Introduction to Bryology*. Macmillan Publishing Co., New York, 431 pp.
- Schuster, R. M. 1984. Evolution, phylogeny and classification of the Hepaticae. In: Schuster, R. M. (ed.). *New Manual of Bryology*, Vol. 2. Hattori Botanical Laboratory, Nichinan, Japan, pp. 892-1070.
- Sillett, S. C. 1991. Canopy bryophyte communities of a lower montane wet forest in Costa Rica: Quantitative sampling in intact forest and isolated trees. M.Sc. thesis, University of Florida, Gainesville.
- Silva, M. P. P. and Pôrto, K. C. 2009. Effect of fragmentation on community structure of epixylic bryophytes in Atlantic forest remnants in the northeast of Brazil. *Biodiv. Conserv.* 18: 317-337.
- Silva-e-Costa, J. D. C., Luiz-Ponzo, A. P., Resende, C. F. D., and Peixoto, P. H. P. 2017. Spore germination, early development and some notes on the effects of *in vitro* culture medium on *Frullania ericoides* (Nees) Mont. (Frullaniaceae, Marchantiophyta). *Acta Bot. Brasil.* 31, available at <http://www.scielo.br/scielo.php?script=sci_arttext&pid=S0102-33062017000100019>.
- Slack, N. G. 1976. Host specificity of bryophytic epiphytes in eastern North America. *J. Hattori Bot. Lab.* 41: 107-132.
- Sporn, S. G., Bos, M. M., and Gradstein, S. R. 2007. Is productivity of cacao impeded by epiphytes? An experimental approach. *Agric. Ecosyst. Environ.* 122: 490-493.
- Sporn, S. G., Bos, M. M., Kessler, M., and Gradstein, S. R. 2010. Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. *Biodiv. Conserv.* 19: 745-760.
- Steege, H. ter and Cornelissen, J. H. C. 1986. Vertical distribution of epiphytes in the rainforest of Guyana, South America. *Symposium Tropical Botany*, Zeist, The Netherlands.
- Steege, H. ter and Cornelissen, J. H. C. 1988. Collecting and studying bryophytes in the canopy of standing rain forest trees. In: Glime, J. M. (ed.). *Methods in Bryology*. Hattori Botanical Laboratory, Nichinan, pp. 285-290.
- Steege, H. ter and Cornelissen, J. H. C. 1989. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21: 331-339.
- Sylvester, S. P., Sylvester, M. D., and Kessler, M. 2014. The world's highest vascular epiphytes found in the Peruvian Andes. *Alp. Bot.* 124: 179-185.
- Thiers, B. M. 1988. Morphological adaptations of the Jungermanniales (Hepaticae) to the tropical rainforest habitat. *J. Hattori Bot. Lab.* 64: 5-14.
- Tixier, P. 1966. *Flore et Végétation Orophiles de l'Ase Tropicale: Les Epiphytes du flanc méridional du Massif Sud Annamitique*. [Orophile flora and vegetation of the Tropical Ase: The epiphytes of the southern flank of the Annamitic South Massif.]. Ph.D. dissertation, Paris.
- Tremblay, R. L. 2008. Ecological correlates and short-term effects of relocation of a rare epiphytic orchid after Hurricane Georges. *Endang. Spec. Res.* 5: 83-90.
- Tweedie, C. E. and Bergstrom, D. M. 1995. A hierarchical approach to studying bryophytic epiphytes in their spatial complex ecosystems. In: *International Bryological Conference. Tropical Bryophytes: Biology, Diversity and Conservation*, Mexico City, 7-12 August 1995, International Bryological Society, pp. 48-49.
- Vital, D. M. and Prado, J. 2006. Moss and liverwort epiphytes on trunks of *Cyathea delgadii* in a fragment of tropical rain forest, Sao Paulo State, Brazil. *Trop. Bryol.* 27: 51-54.
- Werner, F. A. and Gradstein, S. R. 2008. Seedling establishment of vascular epiphytes on isolated and enclosed forest trees in an Andean landscape, Ecuador. *Biodiv. Conserv.* 17: 3195-3207.
- Whitacre, D. 1981. Additional techniques and safety hints for climbing tall trees, and some equipment and information sources. *Biotropica* 13: 286-291.
- Wilding, N., Hedderson, T., Ah-Peng, C., and Magombo, I. 2016. *Bryophytes of Kenya's Coastal Forests. A Guide to the*

- Common Species. Published by authors in electronic format, 66 pp.
- Winkler, S. 1967. Die epiphyllen Moose der Nebelwälder von El Salvador, C. A. [The epiphyllic mosses of the cloud forests of El Salvador, C. A.]. *Rev. Bryol. Lichénol.* 35: 303-369.
- Winkler, S. 1976. Die Hepaticae der Sierra Nevada de Santa Marta, Kolumbien. I. Terrestrische, epixyle und epipetrische Arten. *Rev. Bryol. Lichénol.* 42: 789-827.
- Wolf, J. 1986. Comunidades epiditas en un transecto altitudinal de la Cordillera Central, Colombia. Abstr., IVth Latin-American Botanical Congress, Medellin, Colombia.
- Wolf, J. H. D. 1993a. Epiphyte communities of tropical montane rain forest in the northern Andes. I. Lower montane communities. *Phytocoenologia* 22: 1-52.
- Wolf, J. H. D. 1993b. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Missouri Bot. Gard.* 80: 928-960.
- Wolf, J. H. D. 1993c. Ecology of epiphytes and epiphytes communities in montane rain forests, Colombia. Ph.D. dissertation, University of Amsterdam, The Netherlands.
- Wolf, J. H. D. 1993d. Epiphyte communities of tropical montane rain forest in the northern Andes. II. Upper montane communities. *Phytocoenologia* 22: 53-103.
- Wolf, J. H. D. 1994. Factors controlling the distribution of vascular and nonvascular epiphytes in the northern Andes. *Vegetatio* 112: 15-28.
- Wolf, J. H. D. 1995. Non-vascular epiphyte diversity patterns in the canopy of an upper montane rain forest (2550-3670 m), Central Cordillera Colombia. *Selbyana* 16: 185-195.
- Yanoviak, S. P., Walker, H. A., and Nadkarni, N. M. 2004. Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a Neotropical cloud forest. *Pedobiologia* 48: 51-58.
- Yeaton, R. I. and Gladstone, D. E. 1982. The pattern of colonization of epiphytes on calabash trees (*Crescentia alata* HBK) in Guanacaste Province, Costa Rica. *Biotropica* 14: 137-140.
- Zotz, G. and Vollrath, B. 2003. The epiphyte vegetation of the palm *Socratea exorrhiza* – correlations with tree size, tree age and bryophyte cover. *J. Trop. Ecol.* 19: 81-90.

CHAPTER 8-5

TROPICS: EPIPHYTE

GEOGRAPHIC DIVERSITY

TABLE OF CONTENTS

Diversity	8-5-2
Asia	8-5-5
African Region.....	8-5-11
Neotropics	8-5-17
Summary	8-5-23
Acknowledgments.....	8-5-23
Literature Cited	8-5-23

CHAPTER 8-5

TROPICS: EPIPHYTE GEOGRAPHIC DIVERSITY



Figure 1. Wet forest of Kohala Mountain, Hawaii, with abundant epiphytes. Photo by Melora Purell, through Creative Commons.

Diversity

As is generally true in the tropics, many species have been named multiple times under different names in different countries (Pócs 1984). Hence, understanding the diversity is difficult, as is understanding the bryogeography. As herbaria have become established in more tropical locations, comprehensive studies of various genera and families is untangling some of these taxonomic problems (see, for example, the revision of African *Lepidoziaceae* (Figure 2) by Pócs 1984).



Figure 2. *Bazzania hookeri* (Lepidoziaceae) from the Neotropics. Photo by Michael Lüth, with permission.

Ramsay *et al.* (1987) found seven genera of mosses that occur in all the major rainforest types in Australia: *Macromitrium* (Figure 3), *Racopilum* (Figure 4), *Hymenodon* (Figure 5), *Pyrrhobryum* (Figure 6), *Rhizogonium* (Figure 7), *Sematophyllum* (Figure 8), and *Thuidium* (*Pelekium*?; Figure 9). Epiphyte succession there can occur rapidly in the right microclimate. In the crown, species change from prostrate or small upright plants to large cushion mosses such as *Leptostomum inclinans* (Figure 10). These large mosses occur only on the upper surfaces of branches. But large cushions become unstable, falling to create new habitats. Bark furrows create niches where mosses can become established.



Figure 3. *Macromitrium archeri*, member of a genus of mosses that is in all major rainforests in Australia, forming mats. Photo by David Tng, with permission.



Figure 4. *Racopilum* cf. *cuspidigerum*; *Racopilum* is a genus of mosses that is in all major rainforests in Australia. Photo by Peter Woodard, through Creative Commons.



Figure 5. *Hymenodon pilifer*, member of a genus of mosses that is in all major rainforests in Australia. Photo by Niels Klazenga, with permission.



Figure 6. *Pyrrhobryum paramattense*, member of a genus of mosses that is in all major rainforests in Australia. Photo by David Tng, with permission.



Figure 7. *Rhizogonium* sp., member of a genus of mosses that is in all major rainforests in Australia. Photo by Andras Keszei, with permission.



Figure 8. *Sematophyllum substrumulosum*, member of a genus of mosses that is in all major rainforests in Australia. Photo by J. K. Lindsey, with permission.



Figure 9. *Pelekium* cf. *gratum*, member of a genus of mosses that is in all major rainforests in Australia, forming **wefts**. Photo by Shyamma L., through Creative Commons.



Figure 10. *Leptostomum inclinens* with capsules, a species that forms cushions in the crowns of Australian rainforests. Photo by Clive Shirley, Hidden Forest, with permission.

The **Pterobryaceae** (Figure 21), a family restricted to the tropics, is almost exclusively epiphytic and mostly large, including **dendroid** and **pendent** forms (Churchill & Salazar Allen 2001). Consequently, that family, along with **Neckeraceae** (Figure 11), *Sematophyllum* (Figure 8), and *Taxithelium* (Figure 12), indicates very shady, wet habitats (Pócs 1982). Typically, mosses dominate the base of the trunk, but leafy liverworts, especially the ever-present *Frullania* (Figure 48-Figure 49) and **Lejeuneaceae** (Figure 14), dominate the branches (Pócs 1982; Gradstein 1992).

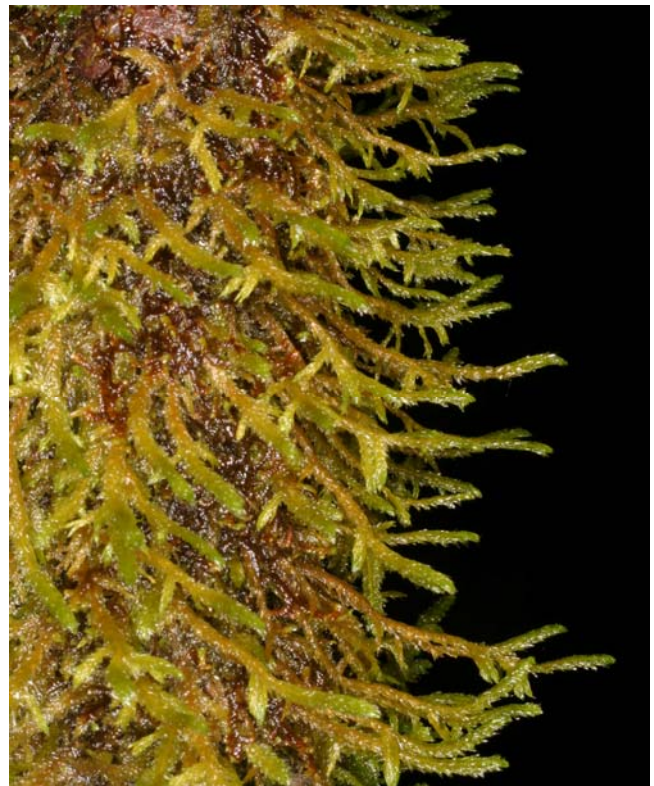


Figure 11. **Neckeraceae** (*Neckera cephalonica*), a family that indicates very shady, wet habitats in the tropics. Photo by Jan-Peter Frahm, with permission.



Figure 12. *Taxithelium planum*; *Taxithelium* indicates very shady, wet habitats in the tropics. Photo by Scott Zona, with permission.

Asia

The **Lejeuneaceae** (Figure 14, Figure 51) is the most abundant and diverse tropical family. In Asia, Gradstein (1991) found 88 species in 17 genera of **Lejeuneaceae**, subfamily **Ptychanthoideae**. This subfamily has more species but fewer genera in Asia than in the Neotropics, and the species in these two floras are very different. Asia is the center of diversity for the tribe **Ptychantheae** (Figure 13); the Neotropics, on the other hand, has its greatest number of species of **Ptychanthoideae** in the tribe **Brachiolejeuneae** (Figure 14). The two floras (Asia vs Neotropics) are distinctly different taxonomically. Gradstein considered the higher species diversity in Asia to be related to the greater latitudinal extension of the rainforest in the Far East. In the Far East, 22% of the **Ptychanthoideae** are non-tropical species, whereas in the Neotropics the non-tropical species are less than 2%.



Figure 13. *Ptychanthus striatus*, tribe **Ptychantheae**, in Thailand. Photo by Soonthree Kornochalert, courtesy of Robbert Gradstein.



Figure 14. *Drepanolejeunea hamatifolia* (**Brachiolejeuneae** in the **Lejeuneaceae**), a genus represented in the Neotropics. Photo by Barry Stewart, with permission.

Gradstein and Culmsee (2010) reported 150 bryophyte species on tree bases of only eight canopy trees in montane Sulawesi (Figure 15), Indonesia. Using only tree bases, they compared bryophyte communities based on tree diameter and bark roughness at a series of elevations. Low elevation bryophytes were characterized by the mosses in **Calymperaceae** (Figure 52-Figure 53), **Fissidentaceae** (Figure 16), **Hypopterygiaceae** (Figure 17-Figure 18), **Leucobryaceae** (Figure 19), **Meteoriaceae** (Figure 20), **Neckeraceae** (Figure 11), **Pterobryaceae** (Figure 21), and **Thuidiaceae** (Figure 9), and the leafy liverworts in **Lejeuneaceae** (Figure 14, Figure 51), **Lophocoleaceae** (Figure 22), **Porellaceae** (Figure 23), and **Radulaceae** (Figure 24).



Figure 15. Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.



Figure 16. *Fissidens pacificus* (Fissidentaceae), in a family that characterizes low-elevation bryophytes. Photo by Jan-Peter Frahm, with permission.



Figure 17. *Hypopterygium didictyon* (Hypopterygiaceae) on tree, in a family that characterizes low-elevation bryophytes. Photo by Juan Larrain, with permission.



Figure 18. *Hypopterygium didictyon* (Hypopterygiaceae), a dendroid moss, in a family that characterizes low-elevation bryophytes. Photo by Felipe Osorio-Zúñiga, with permission.



Figure 19. *Leucobryum boninense* (Leucobryaceae), an epiphytic species in Asia, in a family that characterizes low-elevation bryophytes. Photo by Tomio Yamaguchi, through Creative Commons.



Figure 20. *Floribundaria plumaria* (Meteoriaceae), in a family that characterizes low-elevation bryophytes. Photo by Michael Lüth, with permission.



Figure 21. *Calypothecium duplicatum* (Pterobryaceae), a low elevation genus in Sulawesi, shown here from the Neotropics. Photo by Michael Lüth, with permission.



Figure 22. *Lophocolea cf polychaeta* (Lophocoleaceae) from the Neotropics, in a low-elevation genus in Sulawesi. Photo by Michael Lüth, with permission.



Figure 23. *Porella canariensis* (Porellaceae), a low elevation tropical genus in Sulawesi. Photo by Michael Lüth, with permission.



Figure 24. *Radula flaccida* (Radulaceae) habit with gemmae, in a family that characterizes low-elevation bryophytes. Photo by Michaela Sonnleitner, with permission.

By contrast, bryophytes at higher elevations in Sulawesi (Figure 25) were predominately in the leafy liverwort families **Herbertaceae** (Figure 26), **Lepidoziaceae** (Figure 2), **Mastigophoraceae** (Figure 27-Figure 28), **Scapaniaceae** (Figure 29), **Schistochilaceae** (Figure 30), and **Trichocoleaceae** (Figure 31-Figure 32) (Gradstein & Culmsee 2010). In the submontane and lower montane, **Lejeuneaceae** (Figure 14, Figure 51) has the most species; **Plagiochilaceae** (Figure 33) is also important in the lower montane forest. In the upper montane forest that high diversity is found in the **Lepidoziaceae** (Figure 2). Rough bark is preferred by some species, but none prefer smooth bark. A few species correlate with trunk diameter, but species composition and richness do not. As elevation increases, liverwort species richness generally increases and moss richness decreases. This is a common trend in the tropics. Differences between communities on tree trunks increase with distance, reaching only about 25% similarity between Sulawesi and Borneo. At continental distances, similarity is nearly zero.



Figure 25. Montane mossy cloud forest in Sulawesi, 2300 m at summit of Mt Lokilalaki. Photo courtesy of Robbert Gradstein.



Figure 26. *Herbertus aduncus* (Herbertaceae), member of a family that predominates at high elevations in Sulawesi. Photo from Botany Website, UBC, with permission.



Figure 27. *Mastigophora diclados* (Mastigophoraceae), member of a family that predominates at high elevations in Sulawesi. Photo by Jan-Peter Frahm, with permission.



Figure 28. *Mastigophora flagellifera* (Mastigophoraceae), member of a family that predominates at high elevations in Sulawesi. Photo by Jan-Peter Frahm, with permission.



Figure 29. *Scapania cuspiduligera* (Scapaniaceae) with gemmae, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.



Figure 30. *Schistochila* sp. (Schistochilaceae) in China, member of a family that predominates at high elevations in Sulawesi. Photo by Li Zhang, with permission.



Figure 31. *Trichocolea* sp. from the Neotropics, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.



Figure 32. *Trichocolea* sp. from the Neotropics, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.



Figure 34. Cacao plantation in Sulawesi. Photo courtesy of Robert Gradstein.



Figure 33. *Plagiochila dendroides* (Plagiochilaceae), member of a family that predominates at high elevations in Sulawesi. Photo from Taiwan mosses color illustrations, through Creative Commons.

Ariyanti *et al.* (2008) considered that forest disturbance and land use altered for agriculture was changing the landscape in Central Sulawesi, Indonesia (Figure 34), at a drastic rate. Nevertheless, total bryophyte richness did not differ among forest types. But mosses and liverworts reacted differently. Moss richness was lowest in the cacao agroforests (Figure 34); liverwort richness was equal in all forest types. But in contrast, moss cover was unaffected, whereas liverwort cover decreased significantly in the agroforest. These differences resulted because species composition changed in the cacao agroforests. The more open agroforests were populated by drought-tolerant species. The species composition also differed markedly between large and small trees in the agroforests, but not in the natural forests. The authors suggested that these effects of tree size were due to changes in stemflow of precipitation water.

Kürshner (2008) identified six floral elements in southwest Asia, creating a heterogeneous flora. This included endemics with various origins. There is a very strong tropical influence on the bryophyte flora, particularly of the palaeotropical and Afromontane elements. Nevertheless, nearly 10% (>95 taxa) are of xerotropical origin. Many are unique relicts of a formerly more widely distributed flora and are concentrated primarily in the escarpment mountains of the Arabian Peninsula and Socotra Island.

Magdum *et al.* (2017) collected nine species of corticolous mosses in Panhalgad in the Western Ghats, India, in different seasons, providing the first record of the mosses from the Kolhapur District. These mosses were *Pogonatum microstomum*, *Campylopus flexuosus* (Figure 35), *Leucobryum bowringii* (Figure 36), *Fissidens bryoides* (Figure 37), *Fissidens macrosporoides*, *Loiseaubryum nutans*, *Anomobryum auratum* (Figure 38), *Bryum capillare* (Figure 39), and *Bryum uliginosum* (Figure 40).



Figure 35. *Campylopus flexuosus*, an epiphyte in Panhalgad of the Western Ghats. Photo by Štěpán Koval, with permission.



Figure 36. *Leucobryum bowringii*, an epiphyte in Panhalgad of the Western Ghats. Photo through Creative Commons.



Figure 37. *Fissidens bryoides*, an epiphyte in Panhalgad of the Western Ghats. Photo by Janice Glime.



Figure 38. *Anomobryum auratum* in India, an epiphyte in Panhalgad of the Western Ghats. Photo by Michael Lüth, with permission.



Figure 39. *Bryum capillare*, an epiphyte in Panhalgad of the Western Ghats. Photo by Michael Lüth, with permission.

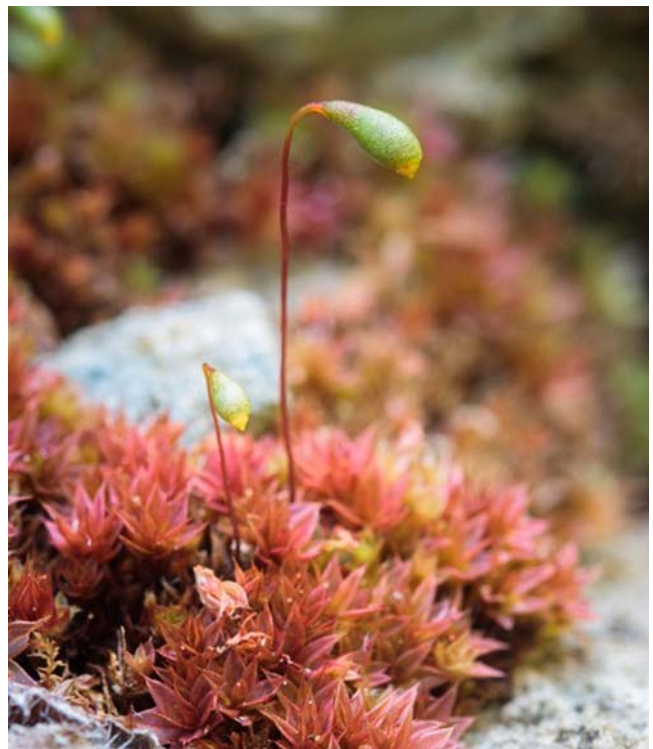


Figure 40. *Bryum uliginosum*, an epiphyte in Panhalgad of the Western Ghats. Photo by Štěpán Koval, with permission.

Kürschner (2003) conducted a phytosociological analysis in southwestern Arabia in the Asir Mountains. The characteristic species are drought-tolerant Afromontane mosses, with *Orthotrichum diaphanum* (Figure 41) and *Syntrichia laevipila* (Figure 42) being most prominent. Life forms and life strategies correlate with the environment. The *Orthotricho-Fabronietum socotranae* (see Figure 43) is a drought-tolerant association that is both xerophytic and tolerant of high light. This formation is dominated by **cushion**, **short-turf**, and **mat-forming perennial stayers** that have regular sporophyte production. The *Leptodonto* (Figure 44)-*Leucodontetum schweinfurthii* (see Figure 45) association is typical of sub-humid areas with **sciophytic** (shade-loving) vegetation. Its bryophytes are liverworts in addition to the mosses that are predominantly tails or fan-forming pleurocarpous perennial

shuttle species. The mosses typically have large spores, adapting them for short-range dispersal that is either passive (with moderately low reproduction) or generative reproduction. This sciophytic group has a much higher diversity of life forms and life strategies than the xerophytic group.



Figure 41. *Orthotrichum diaphanum*, a species of dry locations in the Asir Mountains of southwestern Arabia. Photo by Michael Lüth, with permission.



Figure 42. *Syntrichia laevipila* with capsules, a prominent species in the Asir Mountains in southwestern Arabia. Photo by Michael Lüth, with permission.



Figure 43. *Fabronia* sp.; *Fabronia socotrana* is a prominent epiphytic species in the Asir Mountains in southwestern Arabia. Photo by Michael Lüth, with permission.



Figure 44. *Leptodon smithii*; the *Leptodon* community is typical of the sub-humid area in the Asir Mountains in southwestern Arabia. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 45. *Leucodon treleasei*; the *Leptodonto-Leucodontetum schweinfurthii* community is typical of the sub-humid area of the Asir Mountains in southwestern Arabia. Photo by Jan-Peter Frahm, with permission.

Additional references that may be useful regarding tropical epiphyte diversity in the Asian region include Frahm (1990 – Malaysia), Tixier (1966 – Indonesia), Osada & Amakawa (1956 – Tsushima Islands, Japan).

African Region

Exploration of tropical African bryophytes is relatively new. Augier (1974) listed **corticulous** (growing on bark) bryophytes in the submontane forest of western Cameroon (Figure 46). Akande *et al.* (1982) examined **corticulous** bryophytes in Ibadan, Nigeria. On the 8 phorophytes on two sites they examined, they identified 20 bryophyte species. *Entodontopsis nitens* (Figure 47) is common and present on both sites. They considered *Frullania dilatata* (Figure 48-Figure 49) and *Entodontopsis tenuinervis* to be accidental species. They found the pH of the bryophytes to be similar to that of their bark substrate. In 28 comparisons, 11 bryophyte species combinations have a similarity of 50% or more. *Entodontopsis nitens* and *Pelekium gratum* (Figure 50) have a high degree of association, as do *E. nitens* and *Mastigolejeunea florea* (see Figure 51), *Entodontopsis nitens* and *Erythrodontium barteri*, *Entodontopsis nitens* and *Calymperes palisotii* (Figure 52-Figure 53), and *Erythrodontium barteri* and *M.*

florea. Light is important in determining the height of the bryophytes on the trees. There seems to be no indication of preference for tree species, but the number of trees sampled was limited.



Figure 46. Menchum Falls, NW Province, Cameroon. Photo by Nick Annejohn and family, through public domain.



Figure 47. *Entodontopsis nitens*, a common epiphytic species in Ibadan, Nigeria. Photo from Wilding *et al.* 2016, with permission.



Figure 48. *Frullania dilatata* on smooth bark, a species considered to be accidental in this habitat in Ibadan, Nigeria. Photo by Bernd Haynold, through Creative Commons.

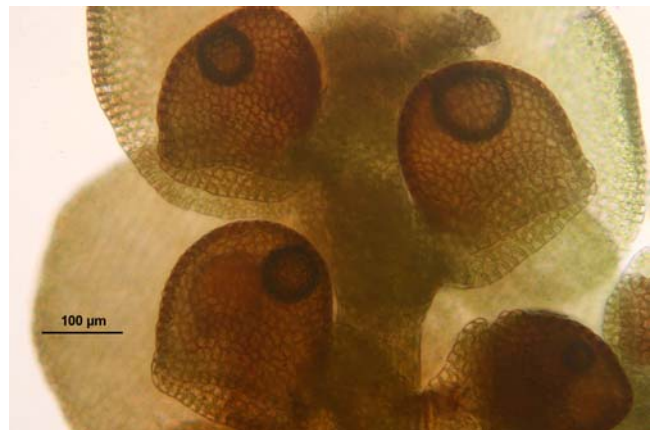


Figure 49. *Frullania dilatata* lobules. Photo by Hermann Schachner, through Creative Commons.



Figure 50. *Pelekium cf. gratum*, a species that shares a 50% similarity index with *Entodontopsis nitens*. Photo by Shyamma L., through Creative Commons.



Figure 51. *Mastigolejeunea repleta*; *M. florea* shares a 50% similarity index with *Entodontopsis nitens*. Photo by Y. M. Wei, courtesy of Robbert Gradstein.



Figure 52. *Calymperes palisotii* on bark. Photo by Scott Zona, through Creative Commons.

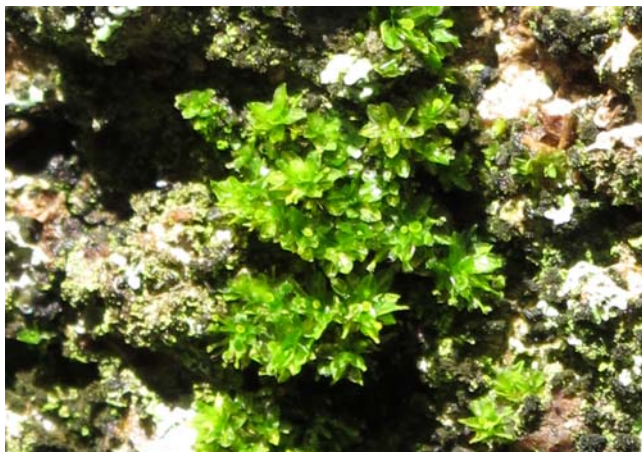


Figure 53. *Calymperes palisotii*, a species that shares a 50% similarity index with *Entodontopsis nitens*. Photo by Scott Zona, through Creative Commons.

Odu (1985) found a greater species richness of epiphytic bryophytes in lowland and freshwater forests than in the mangrove forests of the Niger Delta in Nigeria (Figure 54). He suggested that atmospheric humidity and air impurities may be influencing the bryophytes found. *Calymperes* (Figure 52-Figure 53, Figure 55) and *Octoblepharum* (Figure 56) occur all over the Niger Delta, whereas others are restricted to the lowland freshwater forests. Those in the mangrove forests require adaptations that permit their tolerance of salt water. Further discussion of the mangrove forest is in the subchapter Hydric and Xeric Habitats.



Figure 54. Mangrove roots in the Niger Delta, Nigeria. Photo through Creative Commons.



Figure 55. *Calymperes tenerum*, a common species in the mangrove forests of Thailand. Photo from the Auckland Museum, through Creative Commons.



Figure 56. *Octoblepharum albidum*, a common species in the mangrove forests of Thailand. Photo by M. C. Nair, K. P. Rajesh, and P. V. Madhusoodanan, through Creative Commons.

Akinsoji (1991) reported 26 tracheophytic epiphytes from a tropical rainforest in southwestern Nigeria. As noted elsewhere regarding bryophytes, bark texture makes a difference. Akinsoji found that rough bark is able to collect soil, nutrients, and moisture for epiphytic growth, all features that could benefit bryophytes as well. Trees with smooth bark lacked debris and dust accumulation or moisture retention and had only one or two epiphytes.

More recently, Ezukanma *et al.* (2019a, in review) examined corticolous bryophytes in agroforests of southwestern Nigeria. Only 14 bryophytes were identified. Seven leafy liverwort species were present, but in only two families – **Lejeuneaceae** (Figure 14, Figure 51) and **Radulaceae** (Figure 24). Similarly, seven moss species were found, but they were distributed in five families – **Calymperaceae** (Figure 52-Figure 53), **Entodontaceae** (Figure 57), **Fissidentaceae** (Figure 16), **Hypnaceae** (Figure 58), and **Leucomiaceae** (Figure 59) with one species each, and **Plagiotheciaceae** (Figure 60) with two species. Cashew forests (Figure 61) had eight species, kola (Figure 62) had seven, and cocoa (Figure 63) had six. Only the liverworts *Thysananthus nigrus* (see Figure 64) and *Mastigolejeunea auriculata* (Figure 65) were found in all three forest types. *Entodontopsis nitens* (Figure 47) was the most frequent species, occurring in the kola forest and having a frequency of 27.6%. Next in frequency were *Mastigolejeunea auriculata* (23.65%) and *Entodontopsis nitens* (18.92%) in the cocoa agroforest.



Figure 57. *Entodon* sp. (Entodontaceae); this family is frequent on trees in the agroforests of Nigeria. Photo by Cindy Hough, through Creative Commons.



Figure 58. *Chryso-hypnum diminutivum* (Hypnaceae) from the Neotropics; this family is frequent on trees in the agroforests of Nigeria. Photo by Michael Lüth, with permission.

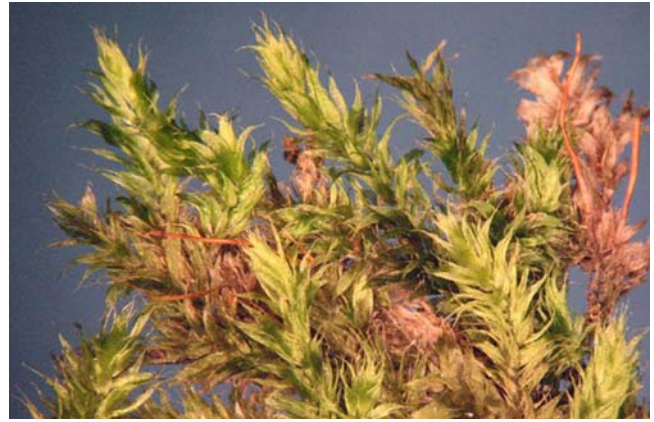


Figure 59. *Leucomium strumosum* (Leucomiaceae), a family that occurs on trees in agroforests in Nigeria. Photo by Claudio Delgadillo Moya, with permission.



Figure 60. *Plagiothecium undulatum* (Plagiotheciaceae), a family that occurs on trees in agroforests in Nigeria. Photo from Proyecto Musgo, through Creative Commons.



Figure 61. Cashew tree in Brazil. Photo by Ben Tavener, through Creative Commons.



Figure 62. Kola (*Cola nitida*) plantation in Malaysia. Photo by Michael Hermann, through Creative Commons.



Figure 63. *Cacao* plantation in Cameroon. Photo by Barada-Nikto, through Creative Commons.



Figure 64. *Thysananthus repletus* (= *Mastigolejeunea repleta*) from China; *Thysananthus nigrus* is present in all three forest types in southwestern Nigeria. Photo by Y. M. Wei, courtesy of Robbert Gradstein.



Figure 65. *Mastigolejeunea auriculata*, a liverwort found in all three of these types of agroforests in Nigeria. Photo by Paul Davison, with permission.

Ezukanma *et al.* (2019b, in press) also assessed the epiphytic bryophytes in the urban agroforests of Ibadan, Nigeria. They studied the corticolous bryophytes up to 2m on the phorophytes of 30 trees in *Citrus* (Figure 66) and *Mangifera* (Figure 67) plantations. Here they identified 19 species, 13 leafy liverworts and 6 mosses. Five species were in both forest types. The mango forests had higher bryophyte diversity and more even distribution of species. The researchers suggested that this might relate to the frequent pruning of the crowns in the mango agroforest. The moss *Calymperes palisotii* (Figure 52-Figure 53) was the most abundant species, especially in the *Citrus* plantations. Corticolous species were generally absent at the base of the phorophyte, occurring with a mean height of 1.39 m (range of 1.17-1.60) on *Mangifera* and 1.11 m (range of 0.48-1.8) on *Citrus*. The moss *Rhacopilopsis trinitensis* (Figure 68) had the highest mean height, extending up to 1.8 m. *Ceratolejeunea beninensis* (see Figure 80-Figure 81) was second in abundance, likewise in the *Citrus* forest. As in the cashew, kola, and cacao forests, *Mastigolejeunea auriculata* (Figure 65; in the *Mangifera* forests) and *Entodontopsis nitens* (in the *Citrus* forests; Figure 47) were species with high frequencies. There were 13 liverwort species, 12 in *Lejeuneaceae* (Figure 14, Figure 51) and 1 in *Jubulaceae* (Figure 69). The six moss species were in four families, with 3 in *Stereophyllaceae* (Figure 47) and 1 each in *Calymperaceae* (Figure 52-Figure 55, Figure 82), *Hypnaceae* (Figure 58), and *Leucomiaceae* (Figure 59). Twelve species occurred in both forest types.



Figure 66. *Citrus* (orange) plantation. Photo by Hans Braxmeier, through Creative Commons.



Figure 67. *Mangifera* (mango) picking, Réunion Island. Photo by B. Navez, through Creative Commons.

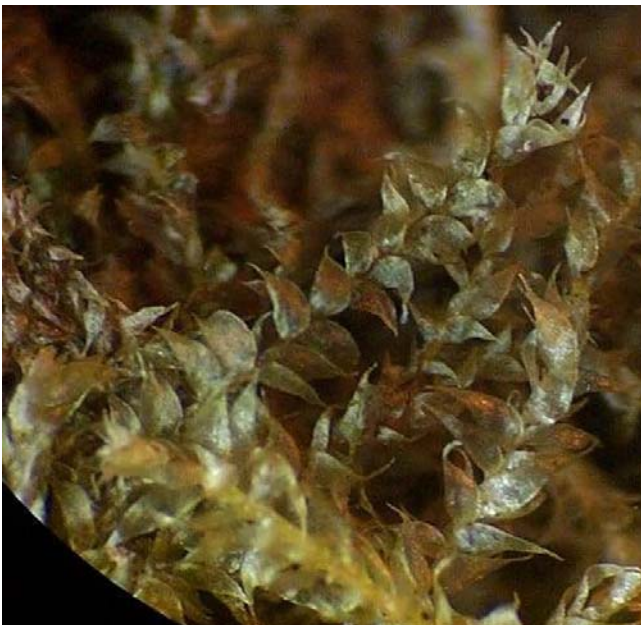


Figure 68. *Rhacopilopsis trinitensis*, the species that reaches the greatest heights on *Mangifera* and *Citrus* phorophytes. Photo by Juan David Parra, through Creative Commons.



Figure 69. *Jubula hutchinsiae* (Jubulaceae), a family that occurs on *Citrus* trees in Nigeria. Photo by Jonathan Sleath, with permission.

Biedinger and Fischer (1996) compared the diversity of epiphytic tracheophytes, bryophytes, and lichens in the montane rainforests and dry forests of Rwanda and Zaïre. They identified 167 species of tracheophytes, 45 of mosses, 82 of liverworts, 78 corticolous lichens, and 57 epiphyllous lichens. While the numbers may be replaced with more recent studies, the proportions are likely to be more accurate.

In South Africa, Dilg and Frahm (1997) explored the epiphytic flora in southern Drakensberg. They found only 38 species, 12 of which were liverworts and 26 were mosses. The *Podocarpus* (Figure 70) forest provides a habitat with high humidity and fire protection; it has the highest number of bryophyte species.



Figure 70. *Podocarpus cunninghamii* trunk with epiphytic bryophytes. Photo by Rudolph89, through Creative Commons.

In addition to these studies, Frahm (1994) reported on ecology of epiphytic bryophytes on Mt. Kahuzi in Zaire. Additional references that may be useful regarding epiphytic diversity in the African tropics include Kürschner (1984 – Saudi Arabia; 1990a – moss societies on Mt. Kinabalu, North Borneo; 1995 – Eastern Congo), Pócs & Szabo (1993 – Mt Elgon, Kenya), Gill & Onyibe (1986 – phytosociology of epiphytes on oil palm in Benin City, Nigeria), Ezukanma (2012 – agroecological corticolous species in southwestern Nigeria). A number of references by Ah-Peng and coworkers will be addressed in other appropriate subchapters of this chapter.

Neotropics

The Neotropics are rich in bryophyte species. In a six-hectare upper montane *Quercus* forest (Figure 71) in Costa Rica, Holz *et al.* (2002) found 206 species, comprised of 100 moss species, 105 liverwort species, and 1 hornwort. They found three main groups of microhabitats in the forest: forest floor, including the tree base; the **phyllosphere** (space surrounding the leaf); other epiphytic habitats. Life forms differ with the humidity and light levels, as discussed in earlier subchapters. Van Reenen (1987) noted that the epiphytic cover of bryophytes in the Andes of Colombia increases with altitude. Wolf (2003) found that the greatest liverwort diversity occurs in the transition zone where two distinct floras are in contact.



Figure 71. *Quercus copeyensis*; in Costa Rica the *Quercus* forest is home to more than 200 bryophyte species. Photo through Creative Commons.

Sillett *et al.* (1995) examined the bryophyte communities of six *Ficus tuerckheimii* (Figure 72) trees in

a Costa Rican lower montane wet forest. They found 109 species on the three intact forest trees and only 76 on the three isolated trees. Of these, 52 species occurred only on the intact forest trees; 18 were only on the isolated trees. Species richness, cover, and frequency of **pendants, tall turfs, tails, and fans** were significantly higher on the trees in the intact forest. Isolated trees had higher rates of evaporation from the inner crowns, more macrolichen cover, and higher levels of sunlight compared to the intact forest trees. Ordination analysis revealed a desiccation gradient ranging from the sheltered intact forest trees to the exposed isolated trees.

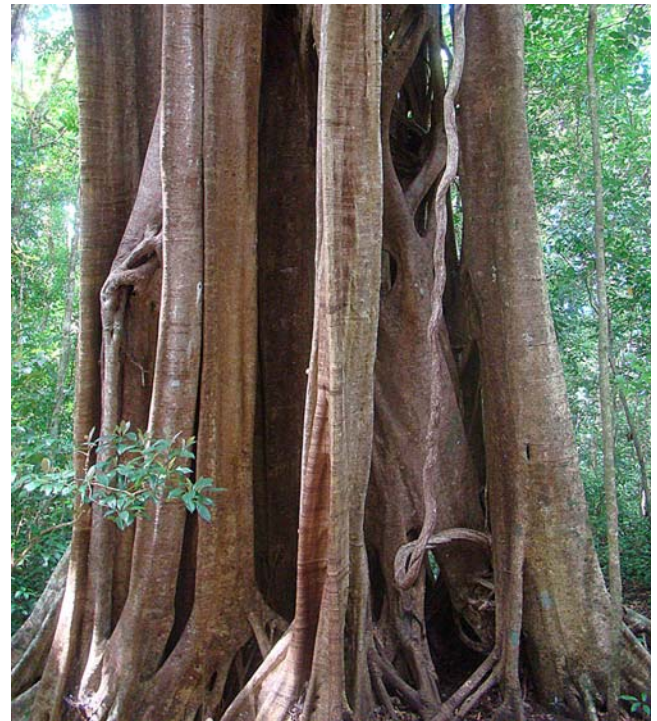


Figure 72. *Ficus tuerckheimii*, Costa Rica. Photo by Dick Culbert, with online permission.

Delia *et al.* (2015) reported 34 epiphytic moss species from El Zancudo, Honduras. They concluded that the montane rainforest that borders Honduras and El Salvador is bryologically diverse, but is largely unexplored.

Richards (1954) considered the Moraballi Creek in Co-operative Republic of Guyana to have four main bryophyte **synusiae** (structural units of major ecological community characterized by relative uniformity of life form or height): high epiphytes, shade epiphytes, epiphylls, dead wood communities. Although these communities are very distinct in both structure and composition, several species, such as *Calymperes lonchophyllum* (see Figure 52-Figure 55) and *Octoblepharum albidum* (Figure 56), occur in all but the epiphyllous synusiae. The epiphyllous species are highly specialized, as will be discussed in a later subchapter. Korpelainen and Salazar Allen (1999) demonstrated genetic variation in three species of *Octoblepharum*, perhaps explaining their ability to occur in multiple community types. Richards (1954) found that Moraballi Creek synusiae differ in their growth (and life) forms of the species, creating differences in community structure. This results in differences between the very dry habitat of the high epiphyte synusiae and the more

moderated shade epiphyte synusia. The latter is characterized by freely projecting or dangling shoots and large thin-walled cells. The Moraballi Creek rainforest bryophyte synusia differ markedly from those of temperate forests by the absence of ground-dwelling bryophyte synusia, the presence of epiphyllous bryophytes, and the preponderance of liverworts, especially **Lejeuneaceae** (Figure 14, Figure 51).

In a semi-deciduous tropical forest of southern Guyana (Figure 73), Sipman (1997) found 100 species of lichens, with 8 out of 14 trees lacking lichens on leaves completely, whereas 3 had 34-46 taxa! Instead, the foliicolous lichens are most likely to grow close to the ground. In contrast to the 34-46 species of lichens on a single tree, they were able to find only 18 bryophyte taxa on canopy leaves.



Figure 73. Guyana waterfall and forest near Paramakatoi. Photo by Kevin Gabbert, through public domain.

Large trees support more species than small ones, with a typical logistic curve of increasing numbers of species related to both plot size and tree **DBH** (diameter at breast height) (Figure 74) (Gradstein *et al.* 1996).

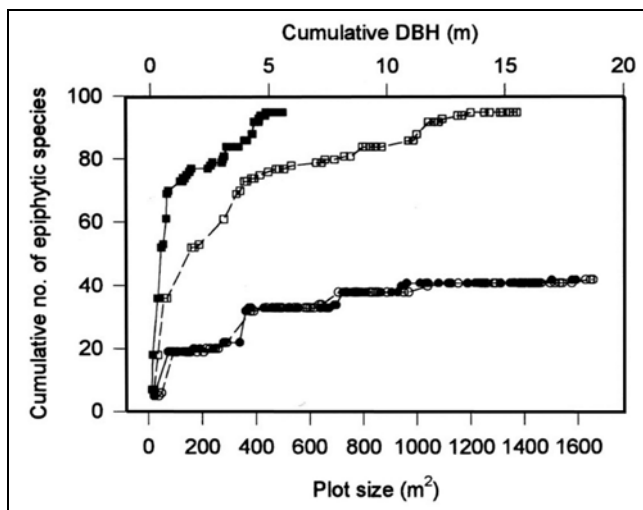


Figure 74. Relationship between number of epiphyte species and plot size and tree DBH in Mexico. Species-area curves are **solid** symbols, cumulative number of species vs cumulative diameter of all trees sampled are **open** symbols. **Squares** represent humid montane cloud forest; **circles** represent humid lowland forest. Modified from Gradstein *et al.* 1996.

Gradstein *et al.* (1990) investigated the epiphytic bryophytes in the dry evergreen forest and mixed forest of the Guianas (Figure 73) using mountaineering techniques. They discovered that the lowland rainforest is not as poor in species as had been thought, once the bryophytes of the canopy are included in the exploration. More than 50% of the local species may occur in the canopy. The mixed forest has the most species. A single tree can support up to 67 species, with 50 species being an average number. The 28 trees sampled supported 154 species of bryophytes. Only a few trees are needed to find most of the species of the local area. Most of the species in this area are rather common, with 80% being widespread in the Neotropics.

In the Colombian Amazon (Figure 75), Campos *et al.* (2015) established 384 plots on 64 trees in four localities. These exhibited 160 species of epiphytic bryophytes, with a preponderance of liverworts (116 species; 44 species of mosses). These included collections from the base to the outer canopy, including 16 trees at each locality. The highest representation of families (Figure 76) included the leafy liverworts **Lejeuneaceae** (Figure 14, Figure 51) (55%) and **Lepidoziaceae** (Figure 2) (8%), and the mosses **Calymperaceae** (Figure 52-Figure 55) (10%), **Octoblepharaceae** (Figure 56) (6%), and **Sematophyllaceae** (Figure 8) (5%). The most common genera were members of **Lejeuneaceae** – **Cheilolejeunea** (Figure 77) (11%), **Pycnolejeunea** (Figure 78) (8%), **Archilejeunea** (Figure 79) (8%), and **Ceratolejeunea** (Figure 80-Figure 81) (8%) – and the moss **Syrrhopodon** (**Calymperaceae**; Figure 82) (7%).



Figure 75. Lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

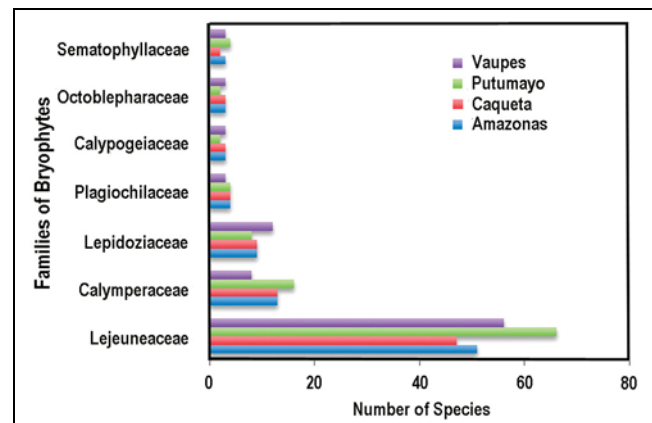


Figure 76. Species richness per family in 4 locations of Colombian Amazon. Modified from Campos *et al.* 2015.



Figure 77. *Cheilolejeunea frangrantissima*, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo by Scott Zona, with permission.



Figure 78. *Pynolejeunea pilifera*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by MNHN – Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.



Figure 79. *Archilejeunea japonica*, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo from Digital Museum, Hiroshima University, with permission.



Figure 80. *Ceratolejeunea cubensis*, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo by Scott Zona, with permission.

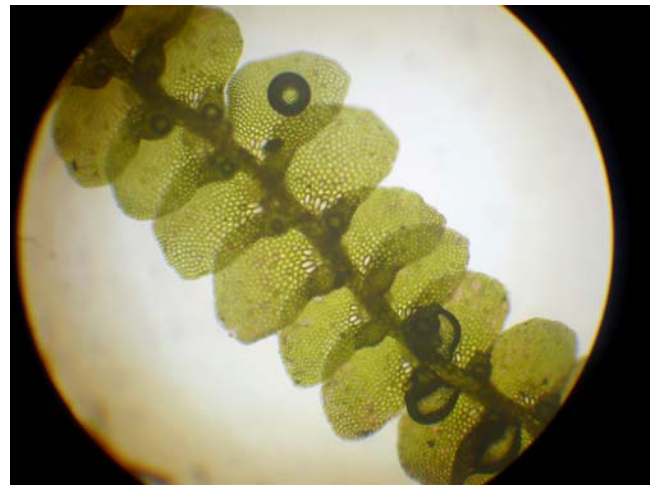


Figure 81. *Ceratolejeunea cubensis*, showing lobules at leaf insertions. Photo by Scott Zona, with permission.

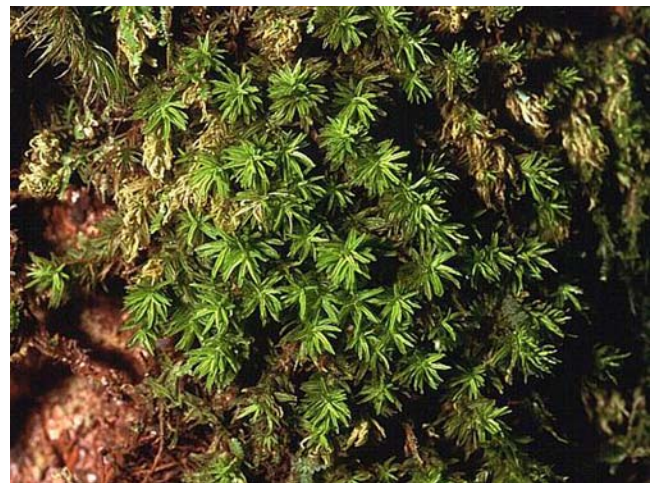


Figure 82. *Syrrhopodon gaudichaudii*, in one of the most common genera in the Colombian Amazon. Photo from Michael Lüth, with permission

Wolf *et al.* (2003) found that the richness per surface area decreases significantly with branch diameter (Figure

83) in the upper montane rainforest of the Cordillera in Colombia. Diversity is highest when the standing crop is at intermediate levels and is negatively correlated with the area of the largest species. On the other hand, **evenness** (similarity of frequencies of different units making up population or sample) is less on older branches. The inner canopy species have the smallest niche widths. When only branch segments are sampled, the vegetation is highly variable, whereas that on whole trees is more uniform. The species follow a species area curve that approaches a flat line after sampling only four trees. The liverworts have the greatest richness in the contact transition zone between two distinct floras. Wolf and coworkers suggested that the arrival time of aggressive competitors such as those that form large patches may be "crucial." Many accidental species maintain a high richness and suggest that dispersal of propagules is important in creating richness.

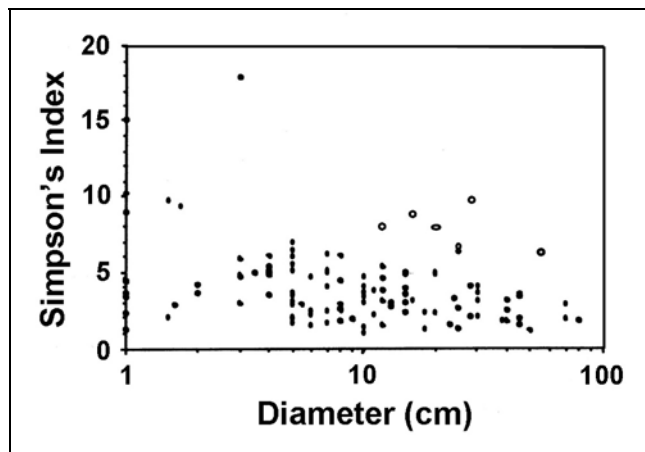


Figure 83. Branch or trunk diameter in the canopy of the upper montane rainforest and Simpson's index of diversity. **Open circles** indicate a group of seven samples that do not adhere to increasing dominance with diameter. Modified from Wolf *et al.* 2003.

In flooded (Figure 84) and "terra firme" (Figure 85) forests of the Colombian Amazon, Benavides *et al.* (2004) found 109 bryophyte species on 14 0.2-ha plots. Mosses and liverworts had opposite responses to moisture, with many more liverworts than moss species in the terra firme, but total richness (mosses + liverworts) differed little between the flooded and non-flooded habitats (Figure 86). The use of the habitat differed between the two forest types, with differences in humidity being the major factor in determining bryophyte communities. Nevertheless, soil was a little-used substrate for both groups in both habitats (Figure 86). Epiphyll species assemblages (*e.g.* Figure 87) were not strongly affected by floodplain vs terra firme. Life forms differed between the two habitat types, with more **fan** and **mat** bryophyte species in the floodplains, and more epiphytic liverworts (hence, almost no **wefts**) in the terra firme forest (Figure 88).



Figure 84. Várzea forest with açai palms, the flooded forest of the Amazon. Photo by Frank Krämer through Creative Commons.



Figure 85. Amazon rainforest, Brazil. Photo by Phil P. Harris, through Creative Commons.

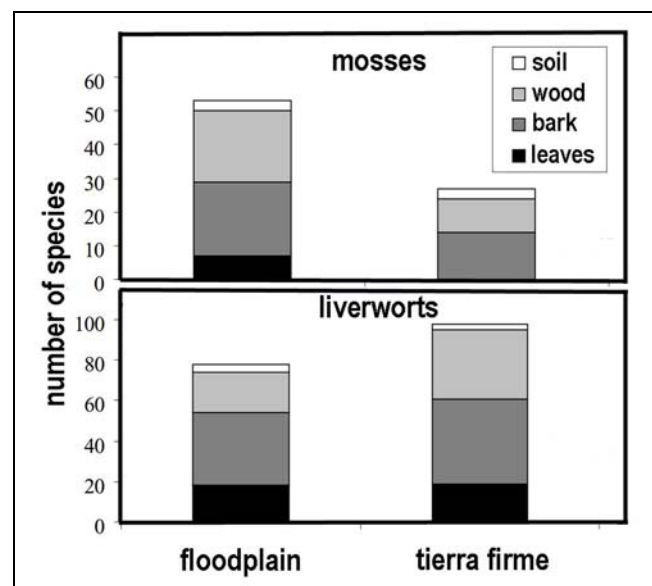


Figure 86. Distribution of bryophyte substrates in terra firme and floodplain in the Aracua region of Colombia. Modified from Benavides *et al.* 2004.



Figure 87. Epiphylls on leaf. Photo by Jessica M. Budke, with permission.

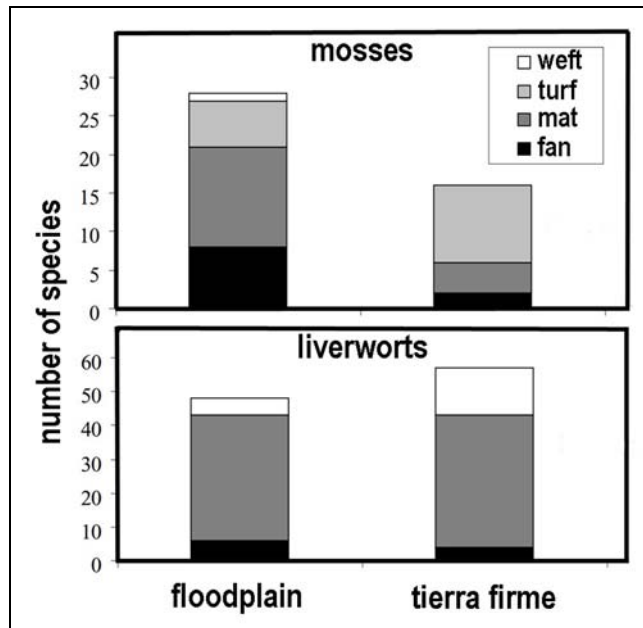


Figure 88. Distribution of bryophyte life forms in tierra firme and floodplain in the Aracuara region of Colombia. Modified from Benavides *et al.* 2004.

Oliveira and ter Steege (2013) determined that epiphytic bryophytes in the tierra firme forests of the Amazon Basin exhibited a typical species abundance distribution (Figure 89).

Kelly *et al.* (2004) described the epiphytic communities of a montane rainforest in the Venezuelan Andes (Figure 90). They surveyed 20 trees, all in a site of only 1.5 ha at 2600 m asl. The non-tracheophyte epiphytes were recorded in 95 sample plots and yielded 22 moss and 66 liverwort species, as well as 46 species of macrolichens. Few of the bryophytes in these communities are **endemic** (native distribution restricted to a certain country or area), although they are mostly restricted to the Neotropics. The dominant bryophyte on the lower trunks is *Syrrhopodon gaudichaudii* (Figure 91), along with the fern *Elaphoglossum hoffmannii* (Figure 92). The intermediate levels are dominated by the leafy liverwort *Omphalanthus filiformis* (Lejeuneaceae; Figure 93) and the orchid *Maxillaria miniata* (see Figure 94). The upper crowns are dominated by the lichens *Usnea* (Figure 95) and *Parmotrema* (Figure 96). Diversity of non-tracheophytes is

greatest in the upper crowns; tracheophyte diversity is greatest at the intermediate levels. As noted in a number of other studies cited herein, similarity is low among plots of the same community, but between-stand and between-plot similarities are relatively high.

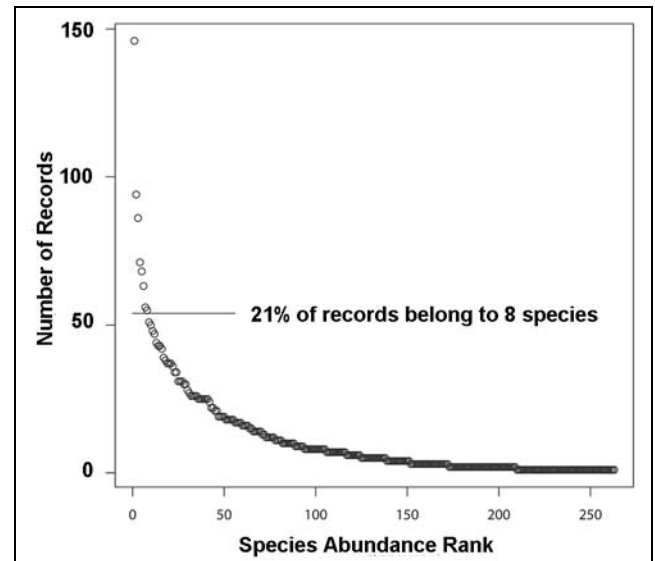


Figure 89. Species abundance distribution based on the complete dataset. Axis x is species ranked by number of records. Modified from Mota de Oliveira and ter Steege 2013.



Figure 90. Montane rainforest in Venezuelan Andes. Photo by Jorge Paparoni, through Creative Commons.



Figure 91. *Syrrhopodon gaudichaudii*, the dominant bryophyte on the lower trunks in a montane rainforest in the Venezuelan Andes. Photo by Michael Lüth, with permission.



Figure 92. *Elaphoglossum hoffmannii*, a fern that typically accompanies *Syrrhopodon gaudichaudii* on lower trunks in montane rainforests in the Venezuelan Andes. Photo by Robbin Moran, with permission.



Figure 93. *Omphalanthus filiformis*, a dominant leafy liverwort at intermediate levels of tree trunks in a montane rainforest in the Venezuelan Andes. Photo by Michael Lüth, with permission.



Figure 94. *Maxillaria molitor*; *Maxillaria miniata* is the dominant flowering plant species, along with the leafy liverwort *Omphalanthus filiformis*, at intermediate levels in the montane rainforest of the Venezuelan Andes. Photo from Megadiverso, through Creative Commons.



Figure 95. *Usnea* from Cumbre Vieja, Canary Islands. Members of this genus dominate the crowns of the montane rainforest in the Venezuelan Andes. Photo by Fährtenleser, through Creative Commons.



Figure 96. *Parmotrema perlatum*. Members of this lichen genus dominate the crowns of the montane rainforest in the Venezuelan Andes. Photo by Alan J. Silverside, with permission.

By comparison, Costa (1999) studied the epiphytic bryophyte diversity of both primary and secondary lowland rainforests in southeastern Brazil, a subtropical region. Unlike many earlier studies, hers included the forest canopy. She found 75 bryophyte species, 39 mosses and 36 liverworts. The highest species richness is exhibited by the mature secondary hillside rainforest, with 43 species. The highly degraded hillside rainforest has the lowest diversity, with only 6 species, and the hillside secondary rainforest with only 5 species. As in so many other studies, the leafy liverwort family *Lejeuneaceae* (Figure 14, Figure 51) is the "most important" with 23 species (30 %) and the moss family *Sematophyllaceae* (Figure 8) with 7 species (10%). Demonstrating the importance of the canopy species in understanding species diversity, Costa found that 45% of the bryophyte species occurred exclusively in the canopy. The most common life form is the **mat**, describing 45% of the species. Forest destruction is more detrimental to shade species than to sun species. Even after 20-45 years, many bryophytes had not returned, but after 80 years the communities were similar to those of primary forest.

In 2017, Gradstein and Benitez added 15 liverwort species to the known flora of Ecuador. They furthermore described two species new to science.

One might not think of looking in a savannah for epiphytes because of the high exposure to sunlight and low moisture. Nevertheless, bryophytic epiphytes do grow there in an Amazonian savanna in Brazil (Figure 97). Gottsberger and Morawetz (1993) found that lichens dominate on the young trees, typically becoming less abundant as the tree ages. Bryophytes are most abundant on older trees and seem to suppress the lichen growth.



Figure 97. Amazonian savannah (Cerrado) in Brazil. Photo by Paulo Q Maio, through Creative Commons.

Additional references that may be useful regarding tropical diversity in the Neotropical epiphytes include Chung (1996 – Panama), Wolf (1993 – Colombia); Jovet-Ast (1949 – groupings of epiphytic mosses in the French West Indies); Frahm (1987a, b – composition of moss vegetation in Peruvian rainforests); Frahm (1987a, c – composition of moss vegetation in Peruvian rainforests).

Summary

Full understanding of the bryogeography of epiphytes is still hampered by our need for comprehensive systematic studies that identify synonyms and demonstrated genetic relatedness.

In Australian tropical rainforests, epiphyte succession is usually rapid, with seven genera occurring in all the major rainforest types: *Macromitrium*, *Racopilum*, *Hymenodon*, *Pyrrhobryum*, *Rhizogonium*, *Sematophyllum*, and *Thuidium* (*Pelekium*?).

In general, the mosses in **Pterobryaceae** and **Neckeraceae** occur as epiphytes throughout the tropics, along with *Sematophyllum* and *Taxithelium*. The liverworts *Frullania* and **Lejeuneaceae** dominate the branches. The tribe **Ptychantheae** is predominant among Asian **Lejeuneaceae**, whereas the tribe **Brachiolejeuneae** predominates in the Neotropics. In Indonesia, the characteristic low-elevation tree-base moss families are **Calymperaceae**, **Fissidentaceae**, **Hypopterygiaceae**, **Leucobryaceae**, **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, and **Thuidiaceae**, and the leafy liverwort families **Lejeuneaceae**, **Lophocoleaceae**, **Porellaceae**, and **Radulaceae**. By contrast the higher elevations have mostly leafy

liverworts in **Herbertaceae**, **Lepidoziaceae**, **Mastigophoraceae**, **Scapaniaceae**, **Schistochilaceae**, and **Trichocoleaceae**. In Africa, **Calymperes** and **Octoblepharum** species occur all over the Niger Delta, whereas in agroforests Ezukanma *et al.* (2019 in review) found only **Lejeuneaceae** and **Radulaceae** among the liverworts, but found five families of mosses. African studies are limited and promise many more species on future expeditions. Bryophyte diversity in the Neotropics is particularly rich and increases with altitude. Intact forests typically have **pendants, tall turfs, tails, and fans**. *Calymperes lonchophyllum* and *Octoblepharum albidum* are common in all communities except as epiphylls. Larger trees support more species than do small ones by providing more niches. For the Neotropics in general, the **Lejeuneaceae** are again the most species-rich family; the most highly represented moss families are **Calymperaceae**, **Octoblepharaceae**, and **Sematophyllaceae**. Fewer endemics occur here compared to those of the flowering plants, and as more systematic studies occur, the number is diminishing.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about.

Literature Cited

- Akande, A. O., Olarinmoye, S., and Egunyomi, A. 1982. Phytosociological studies on some corticolous bryophytes in Ibadan, Nigeria. *Cryptog. Bryol. Lichénol.* 3: 235-248.
- Akinsoji, A. 1991. Studies on the epiphytic flora of a tropical rain forest in southwestern Nigeria. II. The bark microflora. *Vegetatio* 92: 181-185.
- Ariyanti, N. S., Bos, M. M., Kartawinata, K., Tjitrosoedirdjo, S. S., Guhardja, E., and Gradstein, S. R. 2008. Bryophytes on tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia. *Biol. Conserv.* 141: 2516-2527.
- Augier, J. 1974. Bryophytes corticoles a l'etage submontagnard dans l'ouest Camerounais. [Corticolous bryophytes at the submontane stage in western Cameroon]. *Ann. Fac. Sci. Univ. Fed. Cameroun* 17: 97-93.
- Benavides, J. C., Idarraga, A., and Alvarez, E. 2004. Bryophyte diversity patterns in flooded and tierra firme forests in the Araracuara Region, Colombian Amazonia. *Trop. Bryol.* 25: 117-126.
- Biedinger, N. and Fischer, E. 1996. Epiphytic vegetation and ecology in central African forests (Rwanda, Zaire). *Ecotropica* 2: 121-142.
- Campos, L. V., Steege, H. ter, and Uribe, J. 2015. The epiphytic bryophyte flora of the Colombian Amazon. [Los briófitos epífitos de la región Amazónica de Colombia.]. *Caldasia* 37: 47-59.
- Chung, C. C. 1996. Musgos epífitos de un sendero de interpretación, Parque Nacional Altos de Campaña, Panama. Un report preliminar. [Epiphytic mosses of an interpretation trail, Altos de Campana National Park, Panama. A preliminary report.]. *Briolatina* 39: 5-7.

- Churchill, S. P. and Salazar Allen, N. 2001. Mosses. In Gradstein, S. R., Churchill, S. P., and Salazar Allen, N. Guide to the Bryophytes of Tropical America. Mem. N. Y. Bot. Gard. 86: 240-571.
- Costa, D. P. 1999. Epiphytic bryophyte diversity in primary and secondary lowland rainforests in southeastern Brazil. *Bryologist* 102: 320-326.
- Delia, R., Búcaro, R., Touw, A., and Stech, M. 2015. Epiphytic mosses from the understory of a forest in El Zancudo ("Los Bolsones"), La Paz, Honduras. *Bryo. Div. Evol.* 36: 45-50.
- Dilg, C. and Frahm, J.-P. 1997. Untersuchungen zur Flora der epiphytischen Moose der südlichen Drakensberge (Südafrika). Investigations on the flora of the epiphytic mosses of the southern Drakensberg (South Africa). *Trop. Bryol.* 13: 35-45.
- Ezukanma, I. O. 2012. Survey of corticolous bryophytes in selected agroecological sites in Ibadan, Southwestern Nigeria. M.Sc. Thesis. Dept. of Botany. University of Ibadan. xix+95pp
- Ezukanma, I. O., Tessler, M., Salaam, A. M., Chukwuka, K. S., and Ogunniran, A. J. 2019a. Diversity of corticolous bryophytes of selected lowland agroforests in Southwest, Nigeria. (in review).
- Ezukanma, I. O., Tessler, M., Salaam, A. M., Chukwuka, K. S., and Ogunniran, A. J. 2019b. Epiphytic bryophytes of urban agroforests in Ibadan, Southwest, Nigeria. *J. Bryol.* (in press).
- Frahm, J.-P. 1987a. Ökologische Studien an der epiphytischen Moosvegetation in Regenwäldern NE-Perus. [Ecological studies on the epiphytic moss vegetation in rainforests of NO-Peru.] In: *Ergebnisse der BRYOTROP Expedition nach Peru 1982*. Beih. Nova Hedw. 88: 143-158.
- Frahm, J.-P. 1987b. Struktur und Zusammensetzung der epiphytischen Moosvegetation in Regenwäldern NO-Perus. [Structure and composition of epiphytic moss vegetation in rainforests of NO-Peru.] Nova Hedw. Beih. 88: 115-141.
- Frahm, J.-P. 1990. The ecology of epiphytic bryophytes on Mt. Kinabalu, Sabah (Malaysia). *Nova Hedw.* 51: 121-132.
- Frahm, J.-P. 1994. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire). *Trop. Bryol.* 9: 137-152.
- Gill, L. S. and Onyibe, H. I. 1986. Phytosociological studies of epiphytic flora of oil palm (*Elais guineensis*) in Benin City, Nigeria. *Feddes Rep.* 97: 691-695.
- Gottsberger, G. and Morawetz, W. 1993. Development and distribution of the epiphytic flora in an Amazonian savanna in Brazil. *Flora* 188(1): 145-151.
- Gradstein, S. R. 1991. Diversity and distribution of Asian Lejeuneaceae subfamily Ptychanthoideae. *Trop. Bryol.* 4: 1-16.
- Gradstein, S. R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 234-258.
- Gradstein, S. R. and A. Benitez, A. 2017. Liverworts new to Ecuador with description of *Plagiochila priceana* sp. nov. and *Szygiella burghardtii* sp. nov. *Cryptog. Bryol.* 38: 335-348.
- Gradstein, R. and Culmsee, H. 2010. Bryophyte diversity on tree trunks in montane forests of Central Sulawesi, Indonesia. *Trop. Bryol.* 31: 95-105.
- Gradstein, S. R., Montfoort, D., and Cornelissen, J. H. C. 1990. Species richness and phytogeography of the bryophyte flora of the Guianas, with special reference to the lowland forest. *Trop. Bryol.* 2: 117-126.
- Holz, I., Gradstein, S. R., Heinrichs, J., and Kappelle, M. 2002. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. *Bryologist* 105: 334-348.
- Jovet-Ast, S. 1949. Les groupements des muscinées épiphytes aux Antilles françaises. [The groupings of epiphytic mosses in the French West Indies.] *Rev. Bryol. Lichénol.* 18: 682-686.
- Kelly, D. L., O'Donovan, G., Feehan, J., Murphy, S., Drangeid, S. O., and Marciano-Berti, L. 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: Patterns in the distribution of the flora. *J. Trop. Ecol.* 20: 643-666.
- Korpelainen, H. and Salazar Allen, N. 1999. Genetic variation in three species of epiphytic *Octoblepharum* (Leucobryaceae). *Nova Hedw.* 68: 281-290.
- Kürschner, H. 1984. Epiphytic communities of the Asir Mountains (SW Saudi Arabia). *Studies in Arabian bryophytes* 2. *Nova Hedw.* 39: 177-200.
- Kürschner, H. 1990a. Die epiphytischen Moosgesellschaften am Mt. Kinabalu (NordBorneo, Sabah, Malaysia). [The epiphytic moss communities at Mt. Kinabalu (North Borneo, Sabah, Malaysia).] *Nova Hedw.* 51: 1-76.
- Kürschner, H. 2003. Epiphytic bryophyte communities of southwestern Arabia - phytosociology, ecology and life strategies. *Nova Hedw.* 77: 55-71.
- Kürschner, H. 2008. Biogeography of South-West Asian bryophytes - with special emphasis on the tropical element. *Turk. J. Bot.* 32: 433-446.
- Magdum, S. M., Lavate, R. A., Patil, S. M., and Dongare, M. M. 2017. *Biosci. Discov.* 8: 796-801.
- Odu, E. A. 1985. Preliminary studies on the bryophyte flora of the mangrove and fresh water swamp forests in the Niger Delta. In: Wilcox, B. H. D. and Powell, C. P. (eds.). *Proceedings of the Workshop on the Mangrove Ecosystem of the Niger Delta, Port Harcourt (Nigeria), 19-23 May 1980*, pp. 68-87.
- Oliveira, S. M. and Steege, H. ter. 2013. Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. *Acta Bot. Brasil.* 27: 347-363.
- Osada, T. and Amakawa, T. 1956. An observation on the ecological distribution of pendulous bryophytes in the Tsushima Islands. *J. Hattori Bot. Lab.* 17: 52-54.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman & Hall, London, pp. 59-104.
- Pócs, T. 1984. Synopsis of the African Lepidoziaceae K. Müll. *Proceedings of the Third Meeting of the Bryologists from Central and East Europe, Praha, 14-18 June 1982*, Universita Karlova Praha, pp. 107-119.
- Pócs, T. and Szabo, A. 1993. The epiphytic vegetation the endemic giant groundsel (*Senecio barbatipes*) of Mt. Elgon, Kenya. *Opera Bot.* 121: 189-194.
- Ramsay, H. P., Streimann, H., and Harden, G. 1987. Observations on the bryoflora of Australian rain forests. *Symp. Biol. Hung.* 35: 605-620.
- Reenen, G. B. A. van. 1987. Altitudinal bryophyte zonation in the Andes of Colombia: A preliminary report. In: Pócs, T., Simon, T., Tuba, Z., and Podani, J. (eds.). *Proc. IAB Conf. Bryoecology*, *Symp. Biol. Hung.* 35B: 631-637.
- Richards, P. W. 1954. Notes on the bryophyte communities of lowland tropical rain forest, with special reference to Moraballi Creek, British Guiana. *Vegetatio* 6: 319-328.
- Sillett, S. C., Gradstein, S. R., and Griffin, D. III. 1995. Bryophyte diversity of *Ficus* tree crowns from cloud forest and pasture in Costa Rica. *Bryologist* 98: 251-260.

- Sipman, H. J. M. 1997. Observations on the foliicolous lichen and bryophyte flora in the canopy of a semi-deciduous tropical forest. *Abstr. Bot.* 21: 153-161.
- Sjögren, E. 1997. Epiphyllous bryophytes in the Azores Islands. *ARQUIPÉLAGO. Ciências Biol. Marinhas.* [Life Marine Sci.] 15: 1-49.
- Wilding, N., Hedderson, T., Ah-Peng, C., and Malombe, T. 2016. Bryophytes of Kenya's coastal forests: A guide to the common species. Indian Ocean Commission, Biodiversity Project, 58 pp.
- Wolf, J. H. D. 1993. Ecology of epiphytes and epiphytes communities in montane rain forests, Colombia. Ph.D. dissertation, University of Amsterdam, The Netherlands.
- Wolf, J. H. D. 2003. Diversidad y ecología de comunidades epifíticas en la Cordillera Central, Colombia. [Diversity and ecology of epiphytic communities in the Cordillera Central, Colombia.]. *Studies on tropical Andean Ecosystems.* Kramer, Vaduz, Alemania, 502 pp.
- Wolf, J. H., Hammen, T. van der, and Santos, A. G. dos. 2003. Diversidad y ecología de comunidades epifíticas en la Cordillera Central, Colombia. La Cordillera Central Colombiana. [Diversity and ecology of epiphytic communities in the Cordillera Central, Colombia. The Colombian Central Mountain Range.]. *Transecto Parque Los Nevados. Estudios de Ecosistemas Tropandinos* 5: 453-502. <https://www.researchgate.net/profile/Jan_Wolf2/publication/254770074_Diversidad_y_ecologia_de_comunidades_epifiticas_en_la_Cordillera_Central_Colombia/links/00b7d524049a556fa1000000.pdf>.

CHAPTER 8-7

TROPICS: LOWLAND RAINFORESTS

TABLE OF CONTENTS

Lowland Rainforests	8-7-2
Amazonia Lowlands.....	8-7-7
Terra Firme	8-7-11
Dense Forest	8-7-14
Open Forest without Palms	8-7-14
Open Forest with Palms	8-7-14
Liana Forest	8-7-16
Dry Forest	8-7-16
Restinga	8-7-16
Caatinga	8-7-20
Savannah Vegetation	8-7-22
South Atlantic Islands	8-7-23
Summary	8-7-25
Acknowledgments.....	8-7-25
Literature Cited	8-7-25

CHAPTER 8-7

TROPICS: LOWLAND RAINFORESTS



Figure 1. Amazon rainforest near Manaus, Brazil aerial view. Photo by Neil Palmer, through Creative Commons.

Lowland Rainforests

Undeveloped areas of the humid tropics are characterized by tropical rainforest. As shown by Frahm and Gradstein (1991) there are five tropical rainforest belts and their elevational limits are higher on continents than on islands due to the "mass elevation effect." On the continent the forest line is normally ca. 4,000 m asl but has been lowered to ca. 3,200 m in many places due to human impact, reaching as high as 1,500 m asl near the Equator and up to 700 m at the upper and lower tropical borders (Pócs 1982). The area covered, originally at 12% of Earth's surface, is estimated at only about 5% of Earth's surface now (Butler 2006), and it is still rapidly diminishing.

The lowland tropical rainforests (up to 500 m asl) are characterized by their great height, up to 60 m tall (Pócs 1982), with many evergreen species, particularly in areas that have a dry season. With annual rainfall greater than 1500 mm and an average temperature of 20-27°C (Pócs 1982), with little seasonal change, the trees flourish and the canopy is dense. Thus, the forest floor is characterized by limited light, even for a bryophyte. This unfavorable light level, in particular in the lowland rainforest, is made more unfavorable to bryophytes by the heavy leaf litter

(Gradstein 1992; Delgadillo & Cardenas 2002). The result is that the tropical rainforest floor has lower moss species diversity than in temperate regions (Hallingbäck 1992).

Richards (1954) was among the first to attempt a description of these lowland forests. He recognized four main bryophyte synusia in the Moraballi Creek rainforest of British Guiana: high epiphytes, shade epiphytes, epiphyllae, and dead wood, noting their distinctness in both structure and floristic composition. Nevertheless, few species are very frequent. Exceptions to this are *Calymperes lonchophyllum* (see Figure 2) and *Octoblepharum albidum* (Figure 3); with the exception of the epiphyllous habitat, these two species occur in all the other synusia. The epiphylls are almost entirely highly specialized species exclusive to the phyllosphere. Richards noted that growth/life forms differ among the synusia. He further remarked on the absence of bryophyte synusia on the ground at Moraballi Creek, the presence of an epiphyllous community, and the distinct dominance of liverworts, especially *Lejeuneaceae* (Figure 62-Figure 64). Although he noted that the forest was probably poorer in species than many temperate forests, his basis for this statement did not include knowledge of the diverse canopy bryophytes. Richards further claimed that these

comparisons would likewise apply to the lowland rainforests in Africa or the Indo-Malayan region. They would not, however, apply to the montane forests.



Figure 2, *Calymperes* sp.; *C. lonchophyllum* is a species found in all synusia except epiphyllous at Moraballi Creek rainforest of British Guiana. Photo by Niels Klazenga, with permission.



Figure 3. *Octoblepharum albidum*, a species found in all synusia except epiphyllous at Moraballi Creek rainforest of British Guiana. Photo by Portioid, through Creative Commons.

In lower elevations, below 1500 m, the forest typically has a complex canopy. Trees have a variety of heights, some of which may reach 50-60 m tall. Levels in these forests can be classified as emergent, canopy, understory, and forest floor. This provides a variety of conditions for bryophytes, and often the within-tree diversity is greater than that between trees.

The canopy buffers and protects the lower strata of the forest. It reduces turbulence by absorbing wind energy; in one Costa Rican study, canopy (10 m) wind speeds were 11.3 m sec^{-1} while those on the forest floor (2 m) were 4.0 m sec^{-1} (Lawton 1980). The canopy modifies the temperature by absorbing heat and radiation (Nadkarni 1994). Its leaf surfaces absorb CO_2 and emit water vapor.

It modifies the light quality by absorbing red and transmitting green, and it can reduce light intensity by as much as 98% before it reaches the forest floor (Cachan 1963). But for the canopy dwellers, being near the upper surface means intense sunlight, more temperature and humidity extremes, higher water stress, and a nutrient supply dependent on that in rainfall (Nadkarni 1994).

Although irradiation and desiccation are high in the canopy, the inner canopy affords some protection (Gradstein & Pócs 1989). Hence, dense mats or cushions are able to develop here, including the liverwort *Frullania* (Figure 4) and the moss *Macromitrium* (Figure 5). When it is very humid, **pendent** bryophytes and epiphyllous lichens and liverworts become established. In Bolivia (Figure 6), Acebey *et al.* (2003) found that rough mats appeared almost exclusively in the canopy, apparently requiring the high light intensity. This same restriction of rough mats to the high light zone of the upper canopy occurs in Guyana (Cornelissen & ter Steege 1989), and undoubtedly other areas of the tropics.



Figure 4. *Frullania* sp. in the Neotropics, where it can form dense cushions in the lowland rainforest inner canopy. Photo by Michael Lüth, with permission.



Figure 5. *Macromitrium* sp. (Orthotrichaceae) in the Neotropics, where it can form dense cushions in the lowland rainforest inner canopy. Photo by Michael Lüth, with permission.



Figure 6. Los Yungas La Paz, Bolivia. Photo by Elial Bizannes, through Creative Commons.

Costa (1999) studied the rainforest epiphytes in six forest types in the lowland rainforest of Rio de Janeiro, southeastern Brazil (Figure 7). She found 39 moss species and 36 liverwort species. The highest species richness occurred in the mature secondary hillside rainforest (43 species) whereas the lowest diversity was in the highly degraded hillside rainforest (6 species) and hillside secondary rainforest (5 species). As in Guyana (Cornelissen & Gradstein 1990), Costa found that the **Lejeuneaceae** (Figure 62-Figure 64) was one of the most important families (30% of species), with the moss family **Sematophyllaceae** (Figure 41) being second with 7 species (10%). In this case, 45% of the species were exclusively in the canopy. Mats were the most common life form of the six found there. Shade epiphytes are more susceptible to deforestation damage than are sun epiphytes, with many species not returning after 20-45 years. However, after 80 years, the bryophyte flora has recovered to that of the primary forest.



Figure 7. Rainforest canopy, Brazil. Photo by Ben Sutherland, through Creative Commons.

The Tropical Atlantic Rainforest in southeastern Brazil (Figure 7) has the high diversity of 338 taxa, with 49 families and 129 genera represented, with the altitudinal zones accounting for the richness (Costa & Lima 2005).

As expected, the lowest diversity was in the Lowland Atlantic Rainforest; the highest was in the Montane Atlantic Rainforest. The moss family **Sematophyllaceae** (Figure 41) had 19% of the taxa in the lowland forest, **Meteoriaceae** (Figure 8) had 10% in the montane forests, and **Dicranaceae** (Figure 9) had 18% in the upper montane forests. Taxa with wide distributions in the Neotropics accounted for 40% of the total taxa and were important in all the forests. The taxa restricted to Brazil were second most important in the upper montane and montane forests.



Figure 8. *Papillaria* (Meteoriaceae), a common family of pendant mosses in the montane forests of Brazil. Photo by Pete the Poet, with online permission.



Figure 9. *Campylopus pilifer* (Dicranaceae), a family having 18% of the taxa in the upper montane forests of southern Brazil. Photo by Michael Lüth, with permission.

In Australian rainforests (Figure 10), liverworts usually dominate the bryophytes in lowland vine forests (Ramsay *et al.* 1987). Mosses are the more common bryophytes in wet higher altitudes or valley forests. Such bryophytes as *Chandonanthus* (Figure 11), *Dicnemon* (Figure 12), and *Leptostomum* (Figure 13) can be so heavy when they are wet that they become important in pruning the upper and dead branches.



Figure 10. Rainforest at Daintree, Australia. Photo by Thomas Schoch, through Creative Commons.



Figure 11. *Chandonanthus squarrosus*, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Tom Thekathiyil, with permission.



Figure 12. *Dicnemon* sp. from NZ, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Jan-Peter Frahm, with permission.



Figure 13. *Leptostomum* sp. Seno Courtenay Cape Horn, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Blanka Shaw, with permission.

In Australia, members of the epiphytic and saxicolous (growing on or among rocks) moss genus *Macromitrium* (Figure 5) are found primarily in the rainforest (Figure 10) (Ramsay *et al.* 1987). These reach their greatest diversity in the lower elevation ravine rainforests. These habitats form an archipelago of refugia where the remnant patches of forest occur along the eastern and northern coast of the continent.

Streams often create a habitat suitable for a rich bryophyte flora (Dixon 1935; Shevock *et al.* 2017). At Tenompok in Borneo, smaller shrub and tree vegetation is adorned with thin pendulous mosses and liverworts. Tree trunks are thinly covered, but cushions are nearly absent. However, on the more exposed steeper slopes the small trees have moss and liverwort cushions. At higher elevations, these cushions are dominated by liverworts. Above ~2,000 m, up to ~3,000 m asl, the liverwort *Mastigophora* (Figure 14) and other liverworts provide most of the ground cover in the open ridge forest. In more sheltered places, different liverworts occur. Mosses, while present, are not abundant in the ridge forest. *Sphagnum* (Figure 15) cushions can be found, but not abundantly.



Figure 14. *Mastigophora diclados*; in Borneo, this genus, along with other liverworts, provides most of the ground cover in the open ridge forest. Photo by Cesar Garcia, through Creative Commons.



Figure 15. *Sphagnum junghuhnianum*; *Sphagnum* cushions are present but uncommon in the ridge forests of Borneo. Photo from Taibif, through Creative Commons.

In the Guianas, Pardow *et al.* (2012) described a new type of tropical lowland forest, the tropical lowland cloud forest. This forest type has a high epiphytic bryophyte

species richness. This diversity is facilitated by frequent early morning fog in valley locations. Lowland cloud forests and lowland rainforests differed in the functional composition of bryophytes in the canopy, especially the mid and outer canopy. The cloud forest reached a higher biomass and cover of both bryophytic and tracheophytic epiphytes. It similarly had a greater diversity of bryophyte life forms. the typical cloud forest life forms of **tail**, **weft** and **pendants** were almost completely absent in the lowland rainforests, making life forms an easy way to characterize differences in these two forest types.



Figure 16. Top of lowland rainforest canopy in French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Obregón *et al.* (2011) studied the fog frequency in tropical lowland forests. Its occurrence is frequent in the lowland valleys of central French Guiana (Figure 17). It reaches its maximum before sunrise, with a duration of about 4.6 hours. This fog forms when rain saturates the soil, creating greater evapotranspiration. This morning fog follows an increase in temperature differences between the valleys and hill sites after the sun sets. This increase in fog provides an early morning moisture that provides suitable conditions for photosynthesis while the day is still somewhat cooler, supporting a higher epiphyte diversity in the lowland cloud forest compared to the hills. This fog even makes photosynthesis possible in the early mornings of the dry season.



Figure 17. Lowland fog, French Guiana. Photo by Delome, through Wikimedia Commons.

Amazonia Lowlands

The Amazonian lowlands (Figure 1, Figure 18) include both the dry land (**terra firme**) and the wetlands, including mangrove (Figure 19) forests and estuaries. The latter two are saltwater habitats that are not hospitable for bryophytes. Kürschner and Parolly (1998) reported on the shade epiphytes of the Amazonian lowlands of Peru. Since then a number of studies have contributed to our understanding of the bryoflora of Amazonia.



Figure 18. Canopy of lowland rainforest in the Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.



Figure 19. Mangroves in Dominican Republic. Photo by Rachel Doherty, through Creative Commons.

In 1985, Amazonia occupied nearly 6,000,000 km² of South America (Pires & Prance 1985). Since then, deforestation for agriculture, cattle ranching, and logging has greatly reduced its size (Fearnside 2005; Heckenberger *et al.* 2007; Nepstad *et al.* 2008; Clement *et al.* 2015; Butler 2017). Some of the sub-basins have lost up to 33% since 1970 (RAISG 2015). In 2018, the Amazon Basin of 7,000,000 km² had only 5,500,000 km² covered by the rainforest (Wikipedia 2018). Although these numbers do not seem to agree, they nevertheless indicate that considerable loss of Amazonian lowland rainforest is disappearing.

The Amazonian lowland occurs mostly below 100 m asl and rarely rises above 200 m asl. Classification of the vegetation is based primarily on the topography. Two main types of forest vegetation occur: the **terra firme** (dry land) and the inundated formations [**igapó** (Figure 20) and **várzea** (Figure 21)], terms exclusive to Amazonia and all of which are primarily forest land. In addition, some areas have savannah vegetation, but this is a much smaller percentage of the land. Additional more specialized wetland vegetation types are mangrove swamps, **restinga** (spit and distinct type of coastal tropical and subtropical moist broadleaf forest in eastern Brazil), **buritizal** (periodically inundated palm thicket characterized by buriti – the palm *Mauritia flexuosa*), and **pirizal** (cariacal – extensive, emergent vegetation of small, stagnant lakes and puddles). The terra firme forest occupies the largest percentage of the area in Amazonia.



Figure 20. Igapó in Brazil. Photo by Lisa Cyr, through Creative Commons.



Figure 21. Várzea forest, Marajó, Brazil. Photo by Dayse Ferreira, through Creative Commons.

The lowland forests typically have a strong gradient of humidity and light, with humidity decreasing and light intensity increasing from the ground to the upper canopy (Figure 22-Figure 23) (Leon-Vargas 2001).

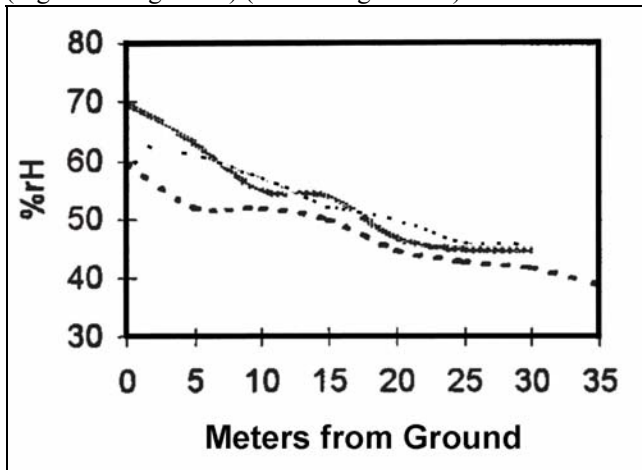


Figure 22. Humidity in ascending heights in the Amazon lowland forest. Modified from Leon-Vargas 2001.

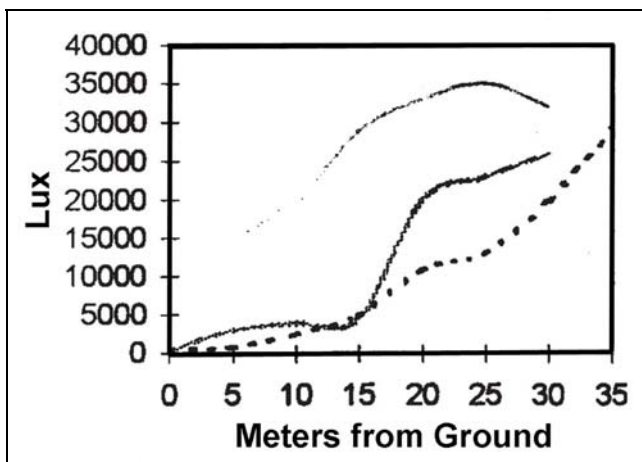


Figure 23. Light intensity at ascending heights in a Neotropical lowland forest. Modified from Leon-Vargas 2001.

Amorim *et al.* (2017) compared bryophyte distribution in southeastern Brazil. They considered two distinct groupings, the inland areas and the coastal areas, with annual precipitation and temperature influencing the

floristic similarity among the coastal areas. Distance from the ocean and altitude were the dominant factors influencing the bryophyte composition of the inland areas.

Lisboa (1976) characterized the Amazonian plain as having poor soil nutrients. Unlike many rainforests, the light intensity can in some areas be very high, resulting in high air (38°C) and soil (42.3°C) temperatures. This combination of high light and high temperatures restricts the bryophyte community. Nevertheless, they found 34 bryophyte species, representing the moss families **Calymperaceae** (Figure 2), **Leucobryaceae** (Figure 40), **Leucodontaceae** (Figure 24), **Plagiotheciaceae** (Figure 25), **Sematophyllaceae** (Figure 41), and liverwort families **Frullaniaceae** (Figure 4, Figure 26), **Lepidoziaceae** (Figure 53), **Lejeuneaceae** (Figure 62-Figure 64), **Odontoschismaceae** (currently included in **Cephaloziaceae**; Figure 27), **Plagiochilaceae** (Figure 28), **Radulaceae** (Figure 73), and **Zoopsidaceae** (currently included in **Lepidoziaceae**; Figure 29). The liverwort *Frullania nodulosa* (Figure 26) stood out as the most frequent species, a species with wide ecological amplitude. Bark of the tree *Aldina heterophylla* (**Rubiaceae**) proved to be a preferred substrate, providing old age, thick bark, and otherwise good conditions for bryophyte community development.



Figure 24. *Antitrichia curtispindula* a member of the **Leucodontaceae**. Photo from Proyecto Musgo through Creative Commons.



Figure 25. *Plagiothecium undulatum*, a member of the **Plagiotheciaceae**. Photo by Christian Peters, with permission.

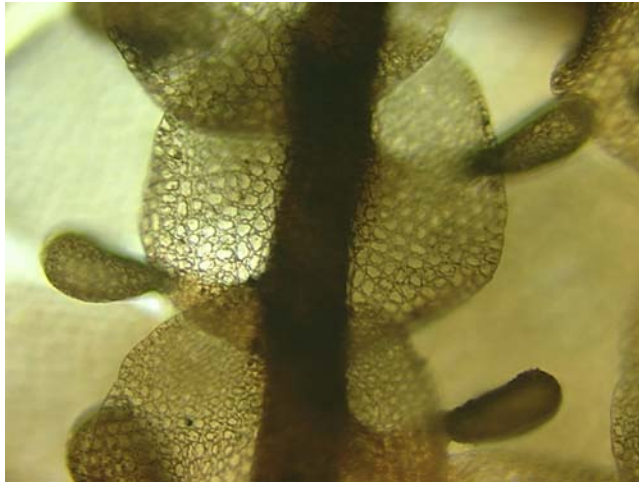


Figure 26. *Frullania nodulosa* underside, the most frequent species in the Amazonian plain. Photo by Matt von Konrat, with permission.



Figure 27. *Odontoschisma longiflorum* (Cephaloziaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 28. *Plagiochila adianthoides* (Plagiochilaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 29. *Zoopsis liukuensis* (Lepidoziaceae, formerly Zoopsidaceae). Members of the Zoopsidaceae are common in the Amazonian lowland rainforests. Photo by Rui-Liang Zhu, with permission.

Benavides *et al.* (2006) claimed the first bryophyte surveys from the Colombian Amazon. They divided the bryophytes into mosses and liverworts and into four life-form classes to describe floodplains, swamps, terra firme forests, and white-sand areas. They identified 50, 45, 45, and 32 species respectively. The higher number of species in the floodplains and swamps suggested the importance of moisture in delimiting communities. **Fan** life forms in the floodplains (Figure 30) further attested to the higher humidity there. Liverworts were more likely to form **mats** in both floodplain and terra firme habitats. And liverworts had greater species richness in the white-sand plots, suggesting a greater importance of light intensity than humidity for these species. Tree bark was the most important substrate for both bryophytes and liverworts in both floodplain and terra firme (Figure 31) (Benavides *et al.* 2004). The floodplain (várzea – Figure 21) differed markedly in species from the other three habitats.

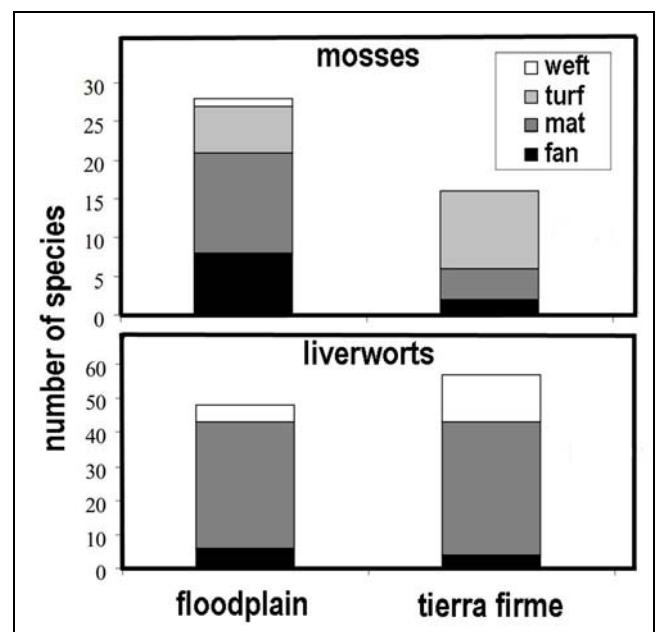


Figure 30. Bryophyte life forms in Terra Firme vs Floodplain. Modified from Benavides *et al.* 2004.

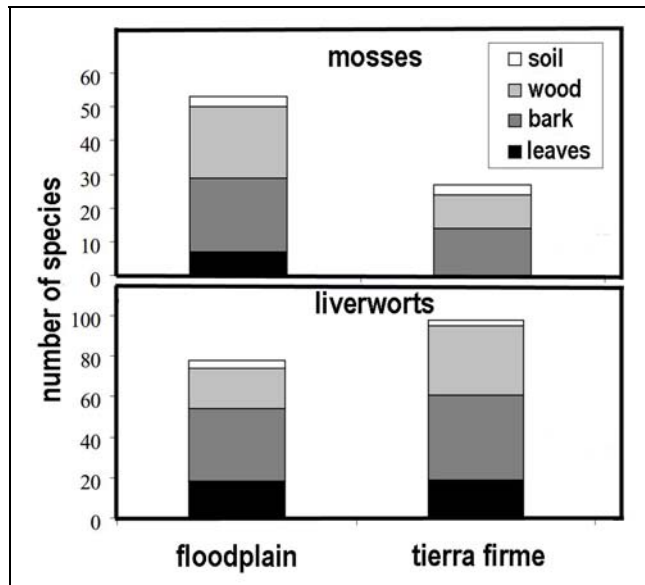


Figure 31. Bryophyte substrates in terra firme vs floodplain. Modified from Benavides *et al.* 2004.

Leal *et al.* (2010) considered the possibility of using bryophytes (and other taxa groups) as surrogate taxa to indicate species richness in the Brazilian Atlantic forest and caatinga. But they did not include the bryophytes in their sampling of the caatinga. They found that the species richness of the various taxa groups (bryophytes, peridophytes, trees, ants, euglossine bees, birds, and mammals; total of 768 species) were significantly correlated with each other. Only two taxa (trees and ants) were required to have excellent surrogacy for species richness of all groups. Bryophytes did not seem to be good surrogates for the richness of the other taxa groupings.

Valente *et al.* (2009) described the mosses in a segment of the Atlantic forest in Bahia State, Brazil. They found 61 moss species, distributed in 23 families. The most species-rich family was **Sematophyllaceae** (7 spp.; Figure 41), followed by **Orthotrichaceae** (6 spp.; Figure 5), **Pilotrichaceae** (5 spp.; Figure 32), **Calymperaceae** (5 spp.; e.g. Figure 2), **Leucobryaceae** (5 spp.; e.g. Figure 40), and **Meteoriaceae** (4 spp.; Figure 8). Corticolous species predominated, with 70% of the species, followed by **epixylous** (on wood with no bark) having 23% of the species. The area was species-rich, with 24% of the bryophytes in the Bahia State represented there.

Epixylic bryophytes (living on logs with no bark) in the Atlantic forest of Brazil supported 35 species of bryophytes, not counting the **Lejeuneaceae** (Figure 62-Figure 64) (Germano & Pôrto 1996, 1997). These comprise 11 families of mosses: **Calymperaceae** (Figure 2), **Pilotrichaceae** (Figure 32), **Fissidentaceae** (Figure 71, Figure 90-Figure 92), **Hookeriaceae** (Figure 33), **Hypnaceae** (Figure 34), **Leucobryaceae** (Figure 40), **Leucomiaceae** (Figure 35), **Orthotrichaceae** (Figure 5), **Plagiotheciaceae** (Figure 28), **Sematophyllaceae** (Figure 41), and **Thuidiaceae** (Figure 36), and 5 families of liverworts: **Aneuraceae** (Figure 55), **Frullaniaceae** (Figure 4), **Geocalycaceae** (Figure 37), **Plagiochilaceae** (Figure 28), and **Radulaceae** (Figure 73). These included 8 species new for northeastern Brazil.



Figure 32. *Cyclodictyon* sp. (**Pilotrichaceae**) in the Neotropics. Photo by Michael Lüth, with permission.



Figure 33. *Hookeria acutifolia* (**Hookeriaceae**), a family that occurs on logs in the Atlantic forest in Brazil. Photo by John Game, through Creative Commons.



Figure 34. *Chryso-hypnum diminutivum* (**Hypnaceae**), a family that occurs on logs in the Atlantic forest in Brazil. Photo by Michael Lüth, with permission.

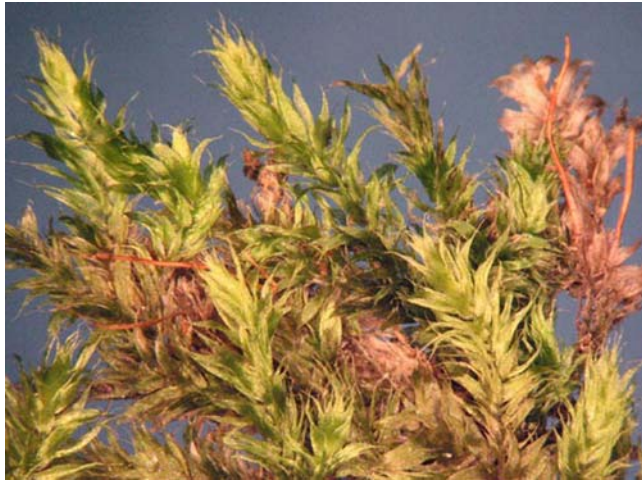


Figure 35. *Leucomium strumosum* (Leucomiaceae), a family that occurs on logs in the Atlantic forest in Brazil. Photo by Claudio Delgadillo Moya, with permission.



Figure 36. *Cyrto-hypnum involvens* (Thuidiaceae) on a log in the Neotropics. Photo by Michael Lüth, with permission.



Figure 37. *Geocalyx graveolens* (Geocalycaceae), a widespread species in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Michael Lüth, with permission.

Pires and Prance (1985) considered the dense tropical forests of the Amazon to be fireproof. These dense forests create many niches, permitting the occurrence of many

species. Costa (2003) reported 514 species in the Amazonian rainforest. Nevertheless, only 106 species are known from the state of Acre, Brazil, suggesting that the area has been understudied. After only two field trips, Costa was able to increase the known flora by 50%. These trips yielded 50 species that were new for the state and 10 more that were "interesting." In an earlier study, Vital and Visnadi (1994) reported only 76 species, and at that time 66 were new records for the state of Acre. This report included one hornwort, *Notothylas vitalii* (see Figure 38).



Figure 38. *Notothylas orbicularis*; *Notothylas vitalii* is the only species of *Notothylas* known to Costa in 1985 for the Amazonian lowland rainforest. Michael Lüth, with permission.

New species most likely await us in these forests. Moura *et al.* (2012) noted the abundance of *Lejeunea* (Figure 39) species in the low várzea (Figure 21) forest in lower Amazon, Pará, Brazil, and reported the new species *Lejeunea combuensis*.



Figure 39. *Lejeunea* from the Neotropics, an abundant species in the low várzea of the Amazon. Photo by Michael Lüth, with permission.

Terra Firme

Oliveira and ter Steege (2013) used standardized sampling methods for epiphytic bryophytes in nine localities in the Amazon basin terra firme forests. They sampled five height zones from forest floor to canopy on

eight canopy trees at each locality, generating 3,014 records and 222 species plus 39 morphospecies. As is typical in the tropics, the most common family was **Lejeuneaceae** (Figure 62-Figure 64) (55% frequency), along with the mosses **Calymperaceae** (Figure 2) (8%), **Leucobryaceae** (Figure 40) (4%), and **Sematophyllaceae** (Figure 41) (4%). No geographical gradient was evident in species richness or composition. Nevertheless, richness differences were evident, with the greatest richness in Saül of French Guiana and Tiputini of Ecuador, compared to other localities. Of the 155 species occurring in more than one locality, 57 were specialists. A total of 29 species were found only in the canopy.



Figure 40. *Leucobryum martianum*. Members of its family, **Leucobryaceae**, are common on trees in the Amazon basin. Photo by Jan-Peter Frahm, with permission.



Figure 41. *Sematophyllum* sp. (**Sematophyllaceae**), a well-represented family from the Amazon lowlands. Photo by Michael Lüth, with permission.

Alvarenga and Lisboa (2009) reported 120 species of bryophytes from the Amazon lowlands. Among these, the **Lejeuneaceae** (Figure 62-Figure 64) species are by far the most abundant with 58 species, followed by **Calymperaceae** (Figure 2) (13 spp.), **Sematophyllaceae** (Figure 41) (9 spp.), and **Plagiochilaceae** (Figure 42). Of these 120 species, 97 are epiphytic; 65 are **epixylic** (growing on wood that has lost its bark). Only 27 species are epiphyllous and only 15 occur on the ground. The most diverse ecosystem is the terra firme forest. The liverworts are strong dominants on leaves, with dominance gradually shifting among the habitats. Liverworts are only slightly dominant on live and dead trunks, and mosses are dominant on the other substrates.



Figure 42. *Plagiochila* sp. from the Neotropics; **Plagiochilaceae** is a common family in the Amazon lowlands. Photo by Michael Lüth, with permission.

Sierra *et al.* (2018) provided a more comprehensive study on the Amazon lowlands, listing 150 species from 712 collections. These were comprised of 109 liverworts and 41 mosses. Of these 104 species lived as epiphytes and 38 as **epiphylls** (species living on leaves). Another 31 species occurred on decaying logs, 16 on rocks, and 24 on soil. But of these species, 68 occurred in only one or two samples. As is obvious from the numbers in each habitat, many were not exclusive to one habitat.

As in many other communities, the most species-rich liverwort families in the studied Amazon lowlands were **Lejeuneaceae** (81 species) and **Lepidoziaceae** (11 species) (Sierra *et al.* 2018). The three most species-rich genera were *Cheilolejeunea* (15 spp.; Figure 43), *Cololejeunea* (12 spp.; Figure 60-Figure 61), and *Ceratolejeunea* (6 spp.; Figure 63), all in the **Lejeuneaceae**. The most common liverwort species were *Cheilolejeunea aneogyna* (see Figure 43), *Pycnolejeunea contigua* (see Figure 44), *Cheilolejeunea neblinensis*, *Cololejeunea surinamensis* (see Figure 60-Figure 61), *Archilejeunea fuscescens* (see Figure 45), *Acrolejeunea torulosa* (see Figure 46), and *Vitalianthus aphanellus*, all in the **Lejeuneaceae**.



Figure 43. *Cheilolejeunea* sp., a species-rich genus in the Amazon lowlands. Photo by Michael Lüth, with permission.



Figure 44. *Pycnolejeunea pilifera*; *Pycnolejeunea contigua* is one of the common species in Amazonian lowlands. Photo from the Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.



Figure 45. *Archilejeunea olivacea*; *Archilejeunea fuscescens* is one of the common species in Amazonian lowlands. Photo by John Braggins, through Creative Commons.



Figure 46. *Acrolejeunea* sp.; *Acrolejeunea torulosa* is one of the common species in Amazonian lowlands. Photo by Peter de Lange, through Creative Commons.

The most species-rich moss families in the studied Amazon lowlands were **Calymperaceae** (16 species), and **Sematophyllaceae** (9 species), again being common families throughout the Neotropics (Sierra *et al.* 2018). The most species-rich genus of mosses was *Syrrhopodon* (12 spp.) in the **Calymperaceae**. The most common moss species were *Leucobryum martianum* (**Leucobryaceae**; Figure 40) and *Syrrhopodon xanthophyllus* (see Figure 47).



Figure 47. *Syrrhopodon lycopodioides* from the Neotropics; *Syrrhopodon xanthophyllus* is one of the two most common moss species in the Amazon lowlands. Photo by Michael Lüth, with permission.

Benavides *et al.* (2006) suggested that the periodic flooding added nutrients to the tree trunks, possibly contributing to the high diversity of bryophytes there compared to the swamps, terra firme forests, and white-sand habitats.

Most of the studies in the Amazon lowlands seem to be floristic with little ecological information on bryophytes. The following habitats can be identified, but few seem to have been described bryophytically, giving us little or no information on dominant species.

Dense Forest

This forest has the greatest biomass of the terra firme forests (Pires & Prance 1985). The understory is distinct, occurring where environmental conditions are optimal. Water is not limiting, having neither too much nor too little.

Open Forest without Palms

This forest has considerably less biomass and trees typically have a basal area of only slightly more than 20 m² per hectare (Pires & Prance 1985). The trees are lower, permitting a greater penetration of light. This allows shrubs and lianas to develop well. Large trees are only occasional. This vegetation type may be limited by a lower water table, impermeability of the soil, poor drainage, poor root penetration, somewhat long dry seasons, or lower relative humidity. Epiphytes are fewer due to the drier habitat. This forest type is not affected by fire and is predominantly not deciduous.

Open Forest with Palms

This forest has a similar physiognomy to that of the open forest without palms, but it has palm trees, especially *Attalea maripa* (Figure 48), *Attalea speciosa* (Figure 49), *Euterpe precatoria* (Figure 50), *Jessenia bataua* (Figure 51), and *Oenocarpus distichus* (Figure 52) (Pires & Prance 1985).



Figure 48. *Attalea maripa*, a palm of the open forest in the Amazonian lowland. Photo by Arria Belli, through Creative Commons.



Figure 49. *Attalea speciosa*, one of the palms found in the open forest of the Amazonian lowlands. Photo by Marcelo Cavallari, through Creative Commons.



Figure 50. *Euterpe precatoria*, one of the palms found in the open forest of the Amazonian lowlands. Photo by Dick Culbert, through Creative Commons.



Figure 51. *Jessenia bataua*, a palm of the open forest in the Amazonian lowland. Photo by Jean-Christophe Pintaud, through Creative Commons.



Figure 52. *Oenocarpus* sp., one of the palms found in the open forest of the Amazonian lowlands. Photo from Kew.org, through Creative Commons.

Van Dunne *et al.* (2001) sampled the epiphytes on the palm *Jessenia bataua* (Figure 51) at 1, 3, and 5 m heights. They found greater similarity among species of bryophytes on the same trunks than they did between palms. Of the 42 species identified, only 3 showed a spatial dependence.

The biomass ratio of mosses to liverworts increased with height on the tree, but total bryophyte biomass showed no significant differences with height. The number of species increased with height sampled. They concluded that short-distance dispersal was less important than long-distance dispersal in determining the species composition. The most abundant families in this palm tree trunk habitat were **Lejeuneaceae** (Figure 62-Figure 64) (13 spp.) and **Lepidoziaceae** (Figure 53) (9 spp.), both leafy liverwort families. The moss family **Leucobryaceae** (Figure 40) was represented by 6 species. The lower and middle tiers of the trunk had mosses in addition to the leafy liverwort families **Calypogeiaceae** (Figure 54) and **Lepidoziaceae**. Only the family **Lejeuneaceae** was typically higher in the higher tiers. In addition, the only other families represented on this palm species were the mosses **Calymperaceae** (Figure 2) and **Sematophyllaceae** (Figure 41) and the thallose liverworts **Aneuraceae** (Figure 55) and **Pallaviciniaceae** (Figure 56).



Figure 53. *Lepidozia cupressina* from the Neotropics; members of the **Lepidoziaceae** occur on the palm *Jessenia bataua* (Figure 51). Photo by Michael Lüth, with permission.

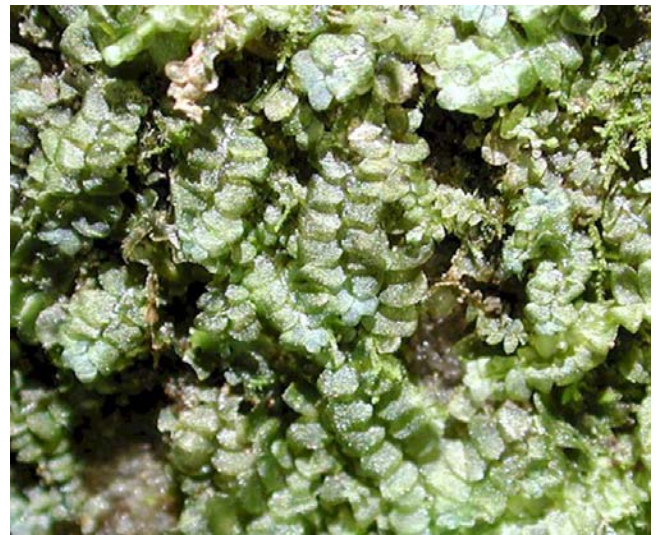


Figure 54. *Calypogeia peruviana* (**Calypogeiaceae**), a family that occurs on the palm *Jessenia bataua* (Figure 51). Photo by Paul Davison, with permission.



Figure 55. *Riccardia fucoidea* (Aneuraceae) from the Neotropics; some members of this family occur on the palm *Jessenia bataua* (Figure 51). Photo by Michael Lüth, with permission.



Figure 56. *Symphyogyna podophylla* (Pallaviciniaceae) with sporophytes; some members of this family occur on the palm *Jessenia bataua* (Figure 51). Photo by Andras Keszei, with permission.

Liana Forest

Lianas occur in the open forest where one might typically find Brazil nut trees (*Bertholletia excelsa*; Figure 57) and *Attalea speciosa* (Figure 49) (Pires & Prance 1985). These forests are usually discontinuous, intermeshed with dense forests lacking lianas. These forests usually are somewhat elevated and have rich deposits of such minerals as iron, aluminium, manganese, nickel, gold, and others. Some bryophytes are able to live on these woody lianas.

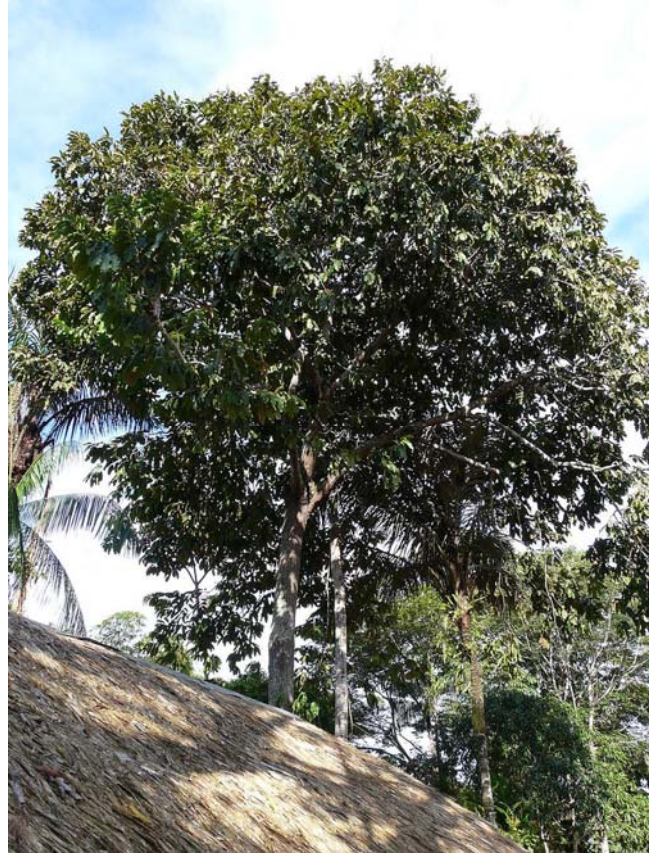


Figure 57. *Bertholletia excelsa*, a dominant tree in the liana forest of Amazonian lowlands. Photo by Vihelik, through public domain.

Dry Forest

The **dry forests** (Figure 58) are transitional forests and are seasonal and drier than rainforests (Pires & Prance 1985). The trees are at least partially deciduous except along the rivers and streams where flooding occurs. These forests do not occupy large areas.



Figure 58. Caatinga rich dry forest. Photo by Duarte, through Creative Commons.

Restinga

The **restinga** is the vegetation of coastal sand dunes. This vegetation type has few species in Amazonia.



Figure 59. Restinga forest at Itaguare beach in Bertioiga State Park, Brazil. Photo by Miguel Rangel Jr., through Creative Commons.

The restinga has received at least some attention regarding its bryophytes. Working in the Setiba State Park, Espírito Santo, Brazil, Visnadi and Vital (1995) found 25 liverwort and 9 moss species, reporting the fewest species in the low and sparse restinga, with the most in the high and sandy restinga. Some of the bryophytes are specific, with the liverworts *Cololejeunea* (syn.=*Aphanolejeunea*) *subdiaphana* (see Figure 60), *Chonecolea doellingeri*, and *Cololejeunea cardiocarpa* (Figure 61) occurring only in the low and sparse restinga. *Leucolejeunea conchifolia* (Figure 62) occurs only in the medium restinga. *Ceratolejeunea laete-fusca* (see Figure 63) was only found in the high restinga; *Taxilejeunea pterigonia* (see Figure 64) only appeared in the high and sandy restinga. The mosses *Bryum capillare* (Figure 65) and *Campylopus pilifer* (Figure 9) only occur in low and sparse restinga; *Groutiella apiculata* (Figure 66) and *Schlotheimia rugifolia* (Figure 67) occur only in the high restinga. In other areas, the restinga bryophyte vegetation can be very different, with few species in common with this one. This is especially true when comparing the northwestern Amazonian restinga bryophyte vegetation with that in the southern Amazonian lowlands.



Figure 60. *Cololejeunea microscopica*; *C. subdiaphana* is found only in the low and sparse restinga in Setiba State Park, Espírito Santo, Brazil. Photo by Stan Phillips, through public domain.



Figure 61. *Cololejeunea cardiocarpa*, a species found only in the low and sparse restinga in Setiba State Park, Espírito Santo, Brazil. Photo by Paul Davison, with permission.



Figure 62. *Leucolejeunea conchifolia*, a species from the medium restinga. Photo by Paul Davison, with permission.



Figure 63. *Ceratolejeunea cubensis*; *C. laete-fusca* occurs only in the high restinga. Photo by Scott Zona, with permission.



Figure 64. *Taxilejeunea* from the Neotropics; *T. pterigonia* occurs only in the high and sandy restinga. Photo by Michael Lüth, with permission.



Figure 67. *Schlotheimia rugifolia*, a species that occurs only in the high restinga in Brazil. Photo by Juan David Parra, through Creative Commons.



Figure 65. *Bryum capillare* with young sporophytes, a species that occurs only in low and sparse restinga. Photo by Michael Lüth, with permission.



Figure 66. *Groutiella apiculata* with capsules, a species that occurs only in the high restinga in Brazil. Photo by Frank Bungartz, through Creative Commons.

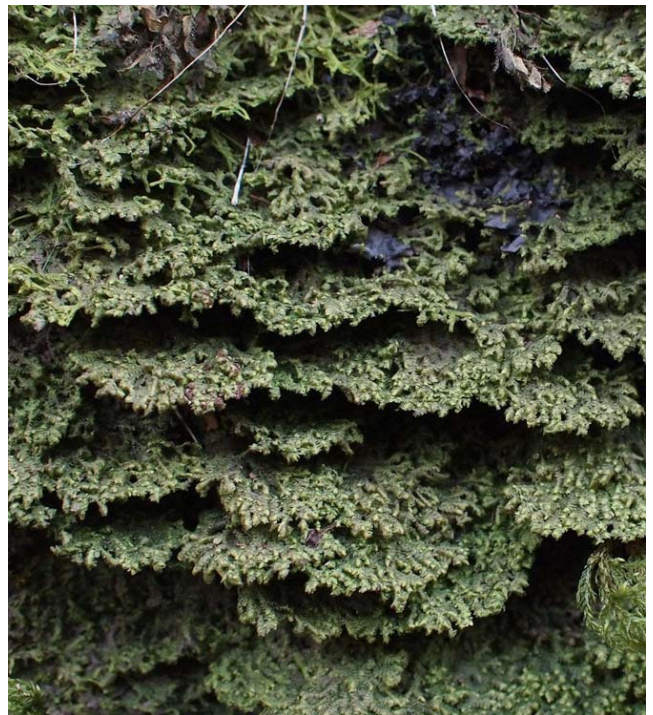


Figure 68. *Jubula hutchinsiae* in Jubulaceae, one of the families with high species richness in Parque Nacional da Restinga de Jurubatiba, RJ, Brazil. Photo by Stan Phillips, through public domain.

In the Parque Nacional da Restinga de Jurubatiba, RJ, Brazil, Imbassahy *et al.* (2009) reported 61 taxa. As is typical in the tropics, the **Lejeuneaceae** (Figure 62-Figure 64) had the most species (25), greatly exceeding other high-species families of **Jubulaceae** (Figure 68-Figure 69) (7), **Calymperaceae** (Figure 2) (4), and **Sphagnaceae** (Figure 70) (4). Most of the taxa are **corticolous** (on bark) and most are of Neotropical distribution (35%). The most common life form is the **mat**.



Figure 69. *Jubula hutchinsiae*, representing the **Jubulaceae**, one of the families with high species richness in Parque Nacional da Restinga de Jurubatiba, RJ, Brazil. Photo by Jonathan Sleath, with permission.



Figure 70. *Sphagnum* sp. from the Neotropics, one of the families with high species richness in Parque Nacional da Restinga de Jurubatiba, Brazil. Photo by Michael Lüth, with permission.

In the restingas of Northeastern Brazil, the soils have a low capacity to retain water, a low nutrient content, and a high salt concentration, coupled with occasions of high temperatures (Silva *et al.* 2016). In the seven areas studied, 55 species were identified. These exhibit intermediate desiccation tolerance and occupy corticolous and ground habitats. This number of species is low compared to other Brazilian restingas. The dominant families are **Lejeuneaceae** (Figure 62-Figure 64) (24 spp.), **Fissidentaceae** (Figure 71) (8 spp.), and **Calymperaceae** (Figure 2) (6 spp.). The families **Metzgeriaceae** (Figure 72), **Plagiochilaceae** (Figure 42), and **Radulaceae** (Figure 73) are absent, whereas they are common in the southeastern restingas. Life forms facilitate their success, with high (**tuft** and **cushion**) or intermediate (**mat** and **carpet**) tolerance to desiccation; the former colonize soil or live trunks, and the latter colonize live trunks and/or, more rarely, decaying trunks. Sun-tolerant species are mostly those with intermediate desiccation that colonize live trunks and decayed logs. There are fewer shade-tolerant species and these are represented by *Fissidens* spp. (Figure

71), which form tufts and have a terrestrial habitat, and by the **pendent** and corticolous *Squamidium nigricans* (Figure 74).



Figure 71. *Fissidens asplenoides*, a common Neotropical species. Photo by Janice Glime.



Figure 72. *Metzgeria conjugata* (**Metzgeriaceae**) British Bryological Society, with permission per Barry Stewart.



Figure 73. *Radula* (**Radulaceae**) in the Neotropics. Photo by Michael Lüth, with permission.



Figure 74. *Squamidium* sp.; *S. nigricans* is a **pendent** moss on bark in the restingas of northeastern Brazil.

Caatinga

This vegetation type of **caatinga** (shrubland; Figure 75) is also known as **campina**, **campinarana**, **chavascal**, and **charravascal** (Pires & Prance 1985). The vegetation grouping grows over leached white sand. This habitat is suitable for forest vegetation, but is limited by the nutrient-poor soil and seasonality of flooding and extreme drought due to the soil (sand) porosity. Diversity is low in a given area, but great variability exists between areas, making the caatingas overall rich in diversity. The caatinga vegetation is **xeromorphic** (having forms adapted to dry habitats). This is exhibited in thick leaves and thick bark. Nevertheless, lichens and mosses are abundant on the branches and soil surface.



Figure 75. Caatinga Biosphere Reserve, Brazil. Photo by Diego Rego Monteiro, through Creative Commons.

When comparing the elevational zones of the **caatinga** (Figure 75) biome in Brazil, Valente *et al.* (2013) found the highest numbers of exclusive bryophyte taxa in the forests and **campos rupestres** (dry, rocky grasslands; Figure 76), accounting for 51% and 40% of the taxa, respectively. The caatinga and cerrado (savanna) had only 5% and 4% respectively. The lower and upper montane zones had the highest species richness and numbers of exclusive taxa. The number of disjunct species was significant between Brazil and the Andes.



Figure 76. Campos rupestres, Brazil, showing dry, rocky grassland. Photo by Antonio José Maia Guimarães, through Creative Commons.

The low elevation Amazon caatinga forest (Figure 77) is an evergreen sclerophyllous forest (Klinge & Herrera 1983). It forms small "islands" in the tall Amazon caatinga. These "islands" are surrounded by a 20-m wide band of vegetation with trees over 10 m tall (**tall bana**). This band resembles the vegetation of the **tall Amazon caatinga**. The low Amazon caatinga is known as **bana**. Klinge and Herrera describe it as an evergreen sclerophyllous woodland with bleached quartz sands in the lowlands of southwestern Venezuela. It occurs as small islands within the tall Amazon caatinga. The outer vegetation belt is about 20 m wide with trees over 10 m tall and this is known as the **tall bana**. Its floristic composition is similar to that of the tall Amazon caatinga. The **low bana** has a maximum tree height that is typically less than 5 m. The central part is occupied by **open bana** where trees are even shorter and very widely spaced.



Figure 77. Caatinga in Brazil. Photo by Glauco Umbelino, through Creative Commons.

Bastos *et al.* (2000) found 65 taxa in the campos rupestres at Estado da Bahia, Brazil. Of these, 41 were mosses and 24 genera were liverworts. Six of the moss species were *Sphagnum* (Figure 70). Consistent with the argument for the need of more studies, 23 of these species are new records for this state.

The first study of bryophytes in Bahia, Brazil, was as recent as 1998 (Bastos *et al.* 1998). In this initial study in the state of Bahia, only 18 species were discovered, 15 mosses and 3 liverworts. These are mainly generalists and **xerophilous** (preferring dry habitat conditions). However, some **hygrophilous** (preferring moist habitats) species occur here. The generalists are represented by *Hyophiladelphus agrarius* (Figure 78-Figure 79), *Hyophila involuta* (Figure 80-Figure 81), *Calymperes palisotii* subsp. *richardii* (Figure 82), *Bryum argenteum* (Figure 83), *Entodontopsis leucostega* (see Figure 84), *Octoblepharum albidum* (Figure 3), *Frullania ericoides* (Figure 85). *Helicophyllum torquatum* (Figure 86) and *Riccia vitalii* (Figure 87) and others are restricted to this type of vegetation. Unlike most of the epiphytic flora, most of these species are erect, acrocarpous species with **short turf** life forms. The leafy liverworts present are **incubous** (leaves overlap from base of stem to tip like shingles of a roof from peak to edge).



Figure 80. *Hyophila involuta* drying, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Bob Klips, with permission.



Figure 78. *Hyophiladelphus agrarius*, a xerophilous generalist in Bahia, Brazil. Photo by Frederick B. Essig, with permission.



Figure 81. *Hyophila involuta* with capsules. Photo by Michael Lüth, with permission.



Figure 79. *Hyophiladelphus agrarius* dry, with capsules. Photo by Frederick B. Essig, with permission.



Figure 82. *Calymperes palisotii*, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Jan-Peter Frahm, with permission.



Figure 83. *Bryum argenteum*, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Michael Lüth, with permission.



Figure 84. *Entodontopsis nitens*; *Entodontopsis leucostega* is a generalist in Brazil. Photo from Wilding *et al.* 2016, with permission.



Figure 85. *Frullania ericoides*, a xerophilous generalist that occurs in Bahia, Brazil. Photo by Blanka Aguero, with permission.



Figure 86. *Helicophyllum torquatum*, a xerophilous generalist that occurs in Bahia, Brazil. Photo by George Shepherd, through Creative Commons.



Figure 87. *Riccia vitalii*, a xerophilous generalist that occurs in Bahia, Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Silva and Pôrto (2016) used mosses to determine if stem growth can be used to indicate changes in local climate change in the caatinga. But the gametophyte length is highly variable in the test moss, *Campylopus pilifer*. They concluded that stem length in this species is a poor indicator of local conditions in harsh environments. On the other hand, soil islands seemed to account for longer stems than typical values for this species.

Savannah Vegetation

Non-forested vegetation in Amazonian Brazil is also known as **campo** (Pires & Prance 1985). These savannahs may have trees or be treeless and are dominated by grasses. The savannahs on terra firme occupy 3-4% of Brazilian Amazonia. The littoral savannahs occur on coastal areas and have frequent lakes. The most common grass is *Paratheria prostrata* (Figure 88). **Roraima savannahs** (Figure 89) are usually open with few trees. **Campos rupestres** (Figure 76) are open formations on rocks and are often confused with open savannahs. These formations suffer drought and are unable to retain water. Lichens are common on the rocks.

Some savannahs are inundated. These are created where sediments are deposited by muddy rivers. Grasses colonize these areas as the rivers recede.



Figure 88. *Paratheria prostrata*, the most common grass in the littoral savannahs. Photo by Ehoarn Bidault, through Creative Commons.



Figure 89. Roraima savannah in Gran Sabana, Venezuela. Photo by Paolo Costa Baldi, through Creative Commons.

South Atlantic Islands

The most recent studies describe the small Brazilian islands in the South Atlantic, Fernando de Noronha and Trindade (Câmara & Carvalho-Silva 2018; Costa *et al.* 2018). Noronha is primarily a caatinga vegetation, but presents some interesting differences in species composition (Costa *et al.* 2018). Like the island of Trindade, there is a lack of endemism on Fernando de Noronha, compared to St. Helena (29 of 110 species), Tristan da Cunha (18 of 160 species), and Ascension (16 of 87 species). Nevertheless, *Riccia ridleyi*, which occurred at just one location, is critically endangered, but during the rainy season, extensive populations can appear (Pereira & Câmara 2015). *Fissidens* (Figure 90-Figure 92) is the most species-rich genus with 12 species. On the other hand, the only member of the *Lejeuneaceae* present is *Lejeunea laetevirens* (Figure 93)! On Trindade, there are 11 species of *Lejeuneaceae*, with a total of 33 bryophyte species. Fernando de Noronha also has more species of mosses (23) compared to liverworts (3) (Costa *et al.* 2018), whereas Trindade has more liverworts (20) compared to mosses (12). Fernando de Noronha island has *Notothyladaceae*

(Figure 94), *Ricciaceae* (Figure 87), *Bryaceae* (Figure 95), *Dicranaceae* (*Dicranella varia*; Figure 96), *Fissidentaceae* (Figure 90-Figure 92), *Pottiaceae* (Figure 79), *Splachnobryaceae* (*Splachnobryum obtusum*; Figure 97), with very low numbers of corticolous species [*Calymperes palisotii* (Figure 82), *Frullania ericoides* (Figure 85), and *Lejeunea laetevirens*]. Many (39%) of the species on this island have worldwide distribution, including *Bryum coronatum* (Figure 95), *Entodontopsis leucostega* (see Figure 84; the only pleurocarpous moss on the island), and *Hyophiladelphus agrarius* (Figure 79). But be careful what you do to preserve species. It is only on a disturbed site with engineering activity that one can find new populations of *Notothylas* (Figure 94), *Fissidens* spp. (e.g. Figure 90-Figure 92), and *Philonotis cernua* (see Figure 98), with the most extensive populations of *Notothylas* occurring there.



Figure 90. *Fissidens bryoides*, a widespread species and one of the 12 species in this genus on Fernando de Noronha. Photo by Dick Haaksma, with permission.



Figure 91. *Fissidens crispus*, a pantropical species and one of the 12 species in this genus on Fernando de Noronha. Photo by Michael Lüth, with permission.



Figure 92. *Fissidens curvatus*, a Neotropical species and one of the 12 species in this genus on Fernando de Noronha. Photo by Des Callaghan, with permission.



Figure 95. *Bryum coronatum*, a widespread species that occurs on Fernando de Noronha. Photo by Paul Siri Wilson, with permission.



Figure 93. *Lejeunea laetivirens*, the only member of **Lejeuneaceae** present on Fernando de Noronha in the South Atlantic. Photo by Scott Zona, through Creative Commons.

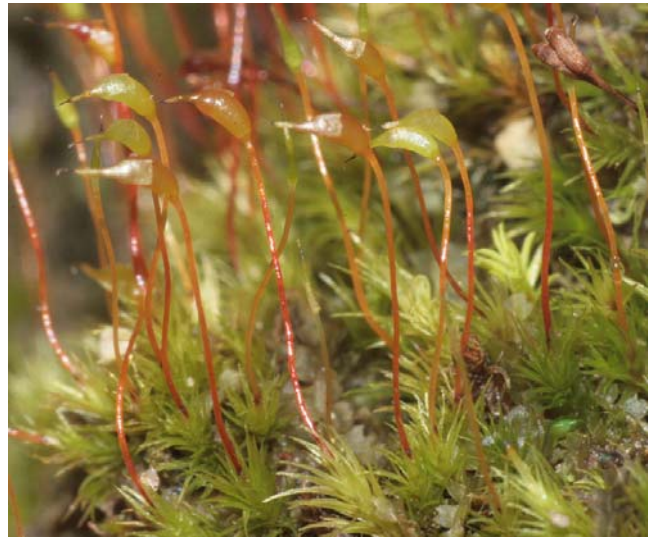


Figure 96. *Dicranella varia* with capsules, a widespread species that occurs on Fernando de Noronha. Photo by Hermann Schachner, through Creative Commons.



Figure 94. *Notothylas orbicularis*, a species that does well on disturbed habitats on Fernando de Noronha. Photo by Štěpán Koval, with permission.



Figure 97. *Splachnobryum obtusum*, a widespread species in the **Splachnobryaceae** and present on Fernando de Noronha. Photo from BBS website, with permission from Barry Stewart.



Figure 98. *Philonotis* sp. from the Neotropics; *Philonotis cernua* occurs on disturbed sites on Fernando de Noronha. Photo by Michael Lüth, with permission.

Summary

Many names are used for lowland rainforests and Amazon rainforests. Some are local names, whereas others are general. Terra (tierra) firme refers to the dryland habitats, thus not including mangroves and other wetlands. It includes dense forest, open forest without palms, open forest with palms, liana forest, dry forest, restinga, caatinga, and savannah, with classification based primarily on topography.

High light intensity and high temperatures limit the bryophyte vegetation in parts of terra firme, but it includes some members of the moss families **Calymperaceae**, **Leucobryaceae**, **Leucodontaceae**, **Plagiotheciaceae**, and **Sematophyllaceae**, and liverwort families **Frullaniaceae**, **Lepidoziaceae**, **Lejeuneaceae**, **Odontoschismaceae** (currently included in **Cephaloziaceae**), **Plagiochilaceae**, **Radulaceae**, and **Zoopsidaceae** (currently included in **Lepidoziaceae**). Logs are an important substrate on terra firme. Otherwise, the most common bryophyte families on terra firme are **Lejeuneaceae**, along with mosses **Calymperaceae**, **Leucobryaceae**, and **Sematophyllaceae**. Other important families are **Calypogeiaceae** and **Lepidoziaceae**, both leafy liverworts. In the drier restinga, the **Lejeuneaceae** predominates among the liverworts, with *Bryum argenteum* and *Campylopus pilifer* among the mosses. In the caatinga, erect generalist, acrocarpous species forming **short turfs** are the most common.

In places with a protracted dry season, like the South Atlantic Islands, **Ricciaceae** are common, going dormant and all but disappearing in the dry season.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about. Tatiany Oliveira da Silva was a tremendous help on this subchapter, providing me with

references and constructive feedback and helping me to understand the various habitats. S. Robbert Gradstein was invaluable in providing me with papers, images, and constructive criticism.

Literature Cited

- Acebey, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.
- Alvarenga, L. D. P. and Lisboa, R. C. 2009. Contribuição para o conhecimento da taxonomia, ecologia e fitogeografia de Briófitas da Amazônia Oriental. *Acta Amazon.* 39: 495-504.
- Amorim, E. T., Carvalho, F. A., Santos, N. D., and Luiz-Ponzo, A. P. 2017. Distribution of bryophytes in south-eastern Brazil: An approach on floristic similarity and environmental filtering. *Cryptog. Bryol.* 38: 3-17.
- Bastos, C. J. P., Albertos, B., and Bôas, S. B. V. 1998. Bryophytes from some Caatinga areas in the state of Bahia (Brazil). *Trop. Bryol.* 14: 69-75.
- Bastos, C. J. P., Yano, O., and Bôas-Bastos, S. B. V. 2000. Briófitas de campos rupestres da Chapada Diamantina, Estado da Bahia, Brasil. [Bryophytes of "campos rupestres" of Chapada Diamantina, state of Bahia, Brazil.]. *Brazil. J. Bot.* 23: 359-370.
- Benavides, J. C., Idarraga, A., and Alvarez, E. 2004. Bryophyte diversity patterns in flooded and terra firme forests in the Araracuara Region, Colombian Amazonia. *Trop. Bryol.* 25: 117-126.
- Benavides, J. C., Duque M., A. J., Duivenvoorden, J. F., and Cleef, A. M. 2006. Species richness and distribution of understorey bryophytes in different forest types in Colombian Amazonia. *J. Bryol.* 28: 182-189.
- Butler, R. A. 2006. Tropical Rainforests of the World. Mongabay.com. Accessed on 5 December 2008 at <<http://rainforests.mongabay.com/0101.htm>>.
- Butler, R. A. 2017. Deforestation drops 16% in the Brazilian Amazon. Mongabay, News & Inspiration from Nature's Frontline. Mongabay Series Global Forests. 19 October 2017. Available at <<https://news.mongabay.com/2017/10/deforestation-drops-16-in-the-brazilian-amazon/>>.
- Cachan, P. 1963. Signification ecologique des variations microclimatiques verticales dans le foret sempervirente de Basse Cote d'Ivoire. *Ann. Fac. Sci. Dakar* 8: 89-155.
- Câmara, P. E. A. S. and Carvalho-Silva, M. 2018. Bryological studies on Trindade Island, South Atlantic. *Field Bryol.* 118: 8-15.
- Clement, C. R., Denevan, W. M., Heckenberger, M. J., Junqueira, A. B., Neves, E. G., Teixeira, W. G., and Woods, W. I. 2015. The domestication of Amazonia before European conquest. *Proc. Royal Soc. B*, 282. Available at <https://www.researchgate.net/publication/280391038_The_Domestication_of_Amazonia_Before_European_Conquest>.
- Cornelissen, J. H. C. and Gradstein, S. R. 1990. On the occurrence of bryophytes and macrolichens in different lowland rainforest types at Maburu Hill, Guyana. *Trop. Bryol.* 3: 29-35.
- Cornelissen, J. H. C. and Steege, H. ter. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.
- Costa, D. P. 1999. Epiphytic bryophyte diversity in primary and secondary lowland rainforests in Southeastern Brazil. *Bryologist* 102: 320-326.

- Costa, D. P. 2003. Floristic composition and diversity of Amazonian rainforest bryophytes in the state of Acre, Brazil. *Acta Amazon.* 33: 399-414.
- Costa, D. P. and Lima, F. M. 2005. Moss diversity in the tropical rainforests of Rio de Janeiro, southeastern Brazil. *Rev. Brasil. Bot.* 28: 671-685.
- Costa, D. P., Henriques, D. K., Silva, M. C., Duckett, J., and Pressel, S. 2018. Bryophytes on Fernando de Noronha island, South Atlantic. *Field Bryol.* 20: 37-48.
- Delgadillo, C. M. and Cardenas, A. S. 1989. Phytogeography of high-elevation mosses from Chiapas, Mexico. *Bryologist* 92: 461-466.
- Dixon, H. N. 1935. A contribution to the moss flora of Borneo. *Bot. J. Linn. Soc.* 50: 60-65.
- Dunné, H. J. F. van, Balcazar, M. P., and Pinzón, M. 2001. Effect of dispersal limitation on small scale spatial structure of epiphytic bryophyte communities in a tropical lowland rain forest (Araracuara, Colombia). Chapt. 5. In: Dunné, H. J. van, Balcazar, M. P., and Pinzón, M. *Tropical Lowland Rain Forest (Araracuara, Colombia)*, pp. 81-94.
- Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: History, rates, and consequences. *Conserv. Biol.* 19: 680-688.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Germano, S. R. and Pôrto, K. C. 1996. Floristic survey of epixylic bryophytes of an area remnant of the Atlantic forest (Timbaúba – PE, Brazil). 1. Hepaticopsida (except Lejeuneaceae) and Bryopsida. *Trop. Bryol.* 12: 21-28.
- Germano, S. R. and Pôrto, K. C. 1997. Ecological analysis of epixylic bryophytes in relation to the decomposition of substrate (Municipality of Timbaúba-Pernambuco, Brazil). *Cryptog. Bryol. Lichénol.* 18: 143-150.
- Gradstein, S. R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). *Bryophytes and Lichens in a Changing Environment.* Clarendon Press, Oxford, pp. 234-258.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems.* Biogeographical and Ecological Studies. Elsevier, Amsterdam, pp. 311-325.
- Hallingbäck, T. 1992. Sveriges boreala mossflora i ett internationellt perspektiv. [The boreal bryophyte flora of Sweden in an international perspective.]. *Svensk Bot. Tidskr.* 68: 177-184.
- Heckenberger, M. J., Russell, J. C., Toney, J. R., and Schmidt, M. J. 2007. The legacy of cultural landscapes in the Brazilian Amazon: Implications for biodiversity. *Philosoph. Trans. Royal Soc. London B Biol. Sci.* 362: 197-208.
- Imbassahy, C. A. A., Costa, D. P., and Araujo, D. S. D. 2009. Briófitas do parque nacional da Restinga de Jurubatiba, RJ, Brasil. *Acta Bot. Brasil.* 23: 558-570.
- Klinge, H. and Herrera, R. 1983. Phytomass structure of natural plant communities on spod-sols in southern Venezuela: The tall Amazon Caatinga forest. *Vegetatio* 53: 65-84.
- Kürschner, H. and Parolly, G. 1998. Shade epiphytic bryophyte communities on the eastern slope of the Andes and in Amazonian lowlands of Peru. *Nova Hedw.* 66: 1-87.
- Lawton, R. 1980. Wind and the ontogeny of elfin stature in a Costa Rican lower montane rainforest. Ph.D. Diss., University of Chicago, Chicago. In Nadkarni 1994.
- Leal, I. R., Bieber, A. G. D., Tabarelli, M., and Andersen, A. N. 2010. Biodiversity surrogacy: Indicator taxa as predictors of total species richness in Brazilian Atlantic forest and Caatinga. *Biodiv. Conserv.* 19: 3347-3360.
- León-Vargas, Y. 2001. Diversity of epiphytic bryophytes in a montane cloud forest in the Venezuelan Andes. Ph.D. Diss., Univ. Bonn.
- Moura, O. S., Ilkiu-Borges, A. L., and Reiner-Drehwald, M. E. 2012. A new species of *Lejeunea* Lib. (Lejeuneaceae) from low várzea forest in lower Amazon (Pará, Brazil). *Nova Hedw.* 95: 197-202.
- Nadkarni, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Amer. Zool.* 34: 70-78.
- Nepstad, D. C., Stickler, C. M., Soares-Filho, B., and Merry, F. 2008. Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point. *Philosoph. Trans. Royal Soc. London B Biol. Sci.* 363: 1737-1746.
- Obregón, A., Gehrig-Downie, C., Gradstein, S. R., Rollenbeck, R., and Bendix, J. 2011. Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity. *Agric. Forest Meteorol.* 151: 290-300.
- Oliveira, S. M. and Steege, H. ter. 2013. Floristic overview of the epiphytic bryophytes of terra firme forests across the Amazon basin. *Acta Bot. Brasil.* 27: 347-363.
- Pardow, A., Gehrig-Downie, C., Gradstein, R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. *Biodiv. Conserv.* 21: 3637-3655.
- Pereira, C. G. and Câmara, P. E. A. S. 2015. Brioflora da ilha de Fernando de Noronha, Brasil. *Pesquisas, Botânica* 67: 149-179.
- Pires, J. M. and Prance, G. T. 1985. The vegetation types of the Brazilian Amazon. Chapt. 7. In: Prance, G. T. and Lovejoy, E. T. *Key Environments: Amazonia.* Pergamon Press, Oxford, pp. 109-145.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology.* Chapman and Hall, London, pp. 59-104.
- RAISG. 2015. Deforestation in the Amazonia (1970-2013). Available at <www.raisg.socioambiental.org>, 48 pp. Deforestation grew by 37% over 13 years and exerts great pressure on the headwaters of Amazonian rivers.
- Ramsay, H. P., Streimann, H., and Harden, G. 1987. Observations on the bryoflora of Australian rain forests. *Symp. Biol. Hung.* 35: 605-620.
- Richards, P. W. 1954. Notes on the bryophyte communities of lowland tropical rain forest, with special reference to Moraballi Creek, British Guiana. *Vegetatio* 6: 319-328.
- Shevock, J. R., Ochrya, R., He, S., and Long, D. G. 2011. *Yunnanobryon*, a new rheophytic moss genus from southwest China. *Bryologist* 114: 194-203.
- Sierra, A. M., Vanderpoorten, A., Gradstein, S. R., Rereira, M. R., Bastos, C. J. P., and Zartman, C. E. 2018. Bryophytes of Jaú National Park (Amazonas, Brazil): Estimating species detectability and richness in a lowland Amazonian megareserve. *Bryologist* 121: 571-588.
- Silva, J. B. and Pôrto, K. C. 2016. Can we use the acrocarpous moss gametophyte length to assess microclimatic conditions in harsh environmental? *Frahmia* 12: 1-15.
- Silva, M. P. P., Zickel, C. S., and Pôrto, K. C. 2016. Bryophyte communities of restingas in Northeastern Brazil and their similarity to those of other restingas in the country. *Acta Bot. Brasil.* 30: 455-461.

- Valente, E. D. B., Pôrto, K. C., Bôas, S. B. V., and Bastos, C. J. P. 2009. Musgos (Bryophyta) de um fragmento de Mata Atlântica na Serra da Jibóia, município de Santa Terezinha, BA, Brasil. [Mosses (Bryophyta) from a fragment of Atlantic Forest in the Jibóia Mountains, Santa Terezinha municipality, Bahia State, Brazil.]. *Acta Bot. Bras.* 23: 369-375.
- Valente, E. D. B., Pôrto, K. C., and Bastos, C. J. P. 2013. Species richness and distribution of bryophytes within different phytophysionomies in the Chapada Diamantina region of Brazil. *Acta Bot. Brasil.* 27: 294-310.
- Visnadi, S. R. and Vital, D. M. 1995. Bryophytes from restinga in Setiba State Park, Espírito Santo. *Trop. Bryol.* 10: 69-74.
- Vital, D. M. and Visnadi, S. R. 1994. Bryophytes of Rio Branco Municipality, Acre, Brazil. *Trop. Bryol.* 9: 69-74.
- Wikipedia. 2018. Amazon rainforest. Last updated 20 June 2018. Accessed 11 July 2018 at <https://en.wikipedia.org/wiki/Amazon_rainforest>.
- Wilding, N., Hedderson, T., Ah-Peng, C., and Magombo, I. 2016. Bryophytes of Kenya's Coastal Forests. A Guide to the Common Species. Published by authors in electronic format, 66 pp.

CHAPTER 8-8

TROPICS: ALTITUDE

TABLE OF CONTENTS

Altitude.....	8-8-2
Defining Zones.....	8-8-9
Zone Limitations	8-8-9
Transplant Studies.....	8-8-11
Latitude vs Altitude.....	8-8-11
Records of Altitude	8-8-14
Diversity-Richness Changes	8-8-17
Dominance Changes.....	8-8-27
Productivity	8-8-31
Adaptations	8-8-32
Life Strategies	8-8-34
Summary	8-8-36
Acknowledgments.....	8-8-36
Literature Cited	8-8-36

CHAPTER 8-8

TROPICS: ALTITUDE



Figure 1. Altitudinal vegetation differences at Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.

Altitude

The changes with elevation are multifold (Figure 1, leading to various hypotheses on the identity of the controlling factors for vegetation. These differences include distinct altitudinal thermal zones, differences in floristic composition and functional forms with both elevation and windward versus leeward slopes, differences in seasonal monsoon wind systems, and isolation of montane forests that cause them to behave like islands (Ohsawa 1995). In addition to these, we will soon see that available moisture is a significant factor. Troll (1948) diagrammed the vegetation zones as they relate to latitude and altitude (Figure 2).

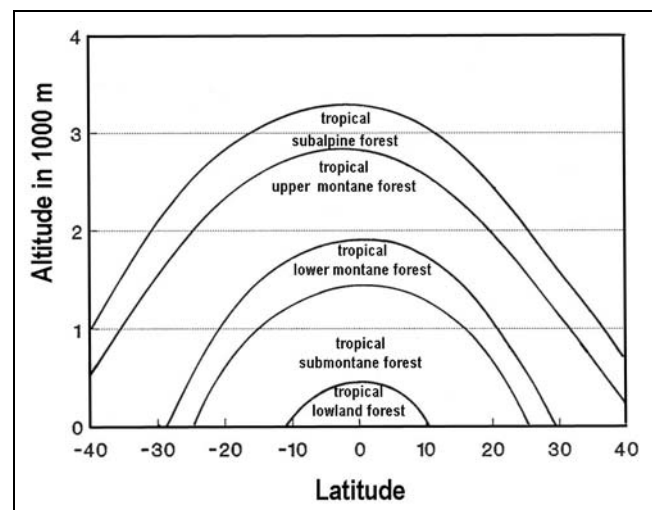


Figure 2. Altitude vs. latitude of vegetational zones. Modified from Troll 1948.

Santos *et al.* (2014) considered the possibility of using liverworts to indicate altitudinal zonation in the Brazilian Atlantic Forest. Among those species found, 34 appeared to be good indicators of the Atlantic Forest groups. Among the 26 localities in the study, the **beta diversity** [ratio between gamma (regional) and alpha (local) diversities, *i.e.* effective number of distinct compositional units in the region] shows a deterministic distribution along the Atlantic coast in southeastern Brazil. Altitude has a significant role in determining the species, with five floristic groups emerging. The important variables are altitude, temperature, and precipitation. But in regions such as oceanic islands and coastal mountains, geographic distance is important.

Santos *et al.* (2017) used a short elevational gradient from 10 m to 1170 m asl in southeastern Brazil to assess changes in bryophyte communities. Using six elevational belts, they sampled ten 10 x 10 m subplots located randomly in a 1-ha forest plot at each elevation in the survey. This revealed 253 species. Richness did not vary significantly with elevation and floristic similarities among the elevations were all greater than 50% except the mountaintop forest, which had a similarity of less than 35%. **Endemism** (ecological state of species being unique to defined geographic location) increased with elevation and amplitudes of the phytogeographical patterns of species decreased as the elevation increased. It is interesting that **dioicous** (sexes on separate plants) species predominated in all elevations sampled and that the smallest dioicous:monoicous ratio was at mid elevations.

At an early date, Seifriz (1924) showed differences in altitudinal distributions of mosses on Mt. Gede, Java (Figure 3). Frahm *et al.* (2003) contended that bryophytes were good indicators of altitudinal zones in rainforests. Based on the reaction of bryophytes to climatic factors, Frahm and coworkers considered the bryophytes to be especially good as indicators of climatic changes. In the tropical rainforests, they have several advantages over flowering plants. The bryophytes are less numerous, have considerably fewer species worldwide, with no more than 5000 species in the Neotropics. Many of the species occur throughout the Neotropics. Recent studies verify the latitudinal diversity gradient in liverworts and hornworts (Figure 4) (Wang *et al.* 2016).



Figure 3. Mount Gede, Java. Photo by Afrogingdahood, through Creative Commons.

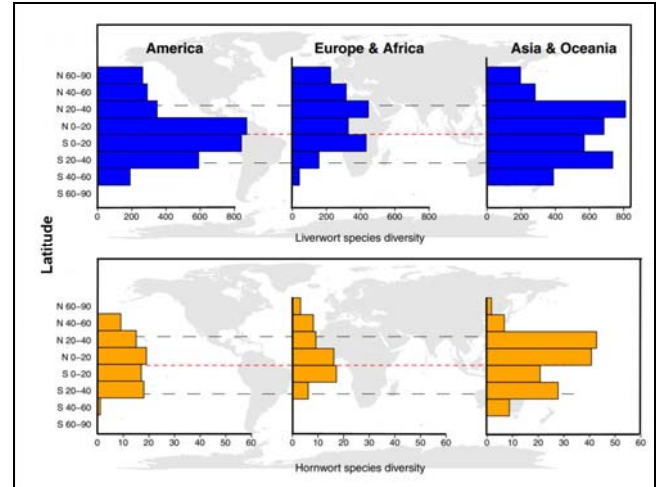


Figure 4. Latitudinal distribution of liverwort and hornwort species richness. Modified from Wang *et al.* (2016).

We find that at greater latitudes the bryophyte communities become more like those at greater elevations near the Equator (Gradstein & Pócs 1989). Comparing high mountains in Colombia, Peru, Borneo, and Papua New Guinea, Gradstein and Frahm (Gradstein & Frahm 1987; Frahm 1990c, d; Frahm & Gradstein 1991) identified similar altitudinal zonations of bryophytes indicating **lowland forest** (Figure 5), **submontane forest**, **upper lower montane forest**, **montane forest** (Figure 6), and **subalpine forest**. These zones seem to be correlated primarily with climate (precipitation, air temperature), rather than with substrate (van Reenen & Gradstein 1983). Bryophyte diversity and abundance both increase from lowlands to montane regions (Figure 7) (van Reenen & Gradstein 1983; Gradstein & Pócs 1989; Frahm 1990b). A similar pattern occurs in Madagascar (Figure 8) (Lewis *et al.* 1996) and Brazil (Pôrto 1992), with an increase in bryophyte and lichen cover and diversity as elevation increases. The distribution patterns of bryophytes through the elevational zones of the humid tropics mimics that of the ferns, which similarly have their highest species numbers in the lower montane forests (Kessler 2000 – Andes, Bolivia & Colombia; Hemp 2002 – Mt. Kilimanjaro, Tanzania).



Figure 5. Lowland rainforest, Rio Dantas, Costa Rica. Photo by Nattox, through Creative Commons.



Figure 6. Montane and upper montane forests, Parque Nacional de Itatiaia, Brazil. Photo by Gabriel R. Vallim.

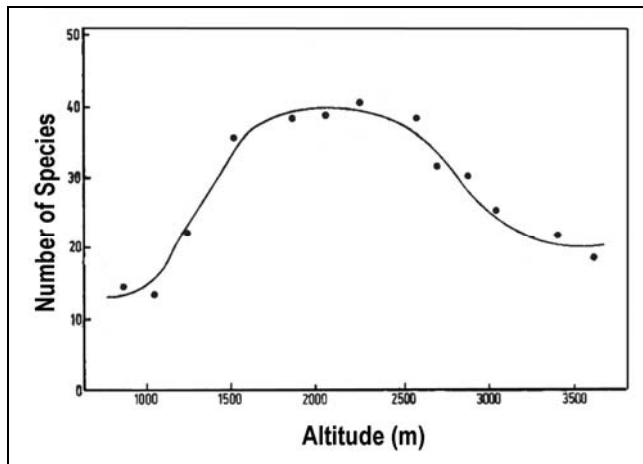


Figure 7. Species curve along an altitudinal transect in Colombia. Modified from van Reenen & Gradstein 1983.



Figure 8. Mountains of Tsingy de Bemaraha, Madagascar. Photo from Travel Tuesdays to Madagascar, through Creative Commons.

Another important observation for the tropical distributions of species with altitude is that for most species the habitat preferences are comparable to those at higher latitudes (Gradstein & Vána 1987). Nevertheless, some occupy quite different habitats in the tropics, such as *Diplophyllum obtusatum* (Figure 9), *Solenostoma sphaerocarpum* (Figure 10), and *Schistochilopsis incisa* (Figure 11). Whereas these may be found in pristine habitats at higher latitudes, they are colonizers of man-

made habitats in the tropics. Some species that are especially common (and typically have relatively wide niches and/or distributions) extend from tropical altitudes to northern habitats. From peat bogs, *Sphagnum magellanicum* (Figure 12) and *S. cuspidatum* (Figure 13) fit this description. Rock outcrops in both latitudinal and altitudinal extremes can have *Racomitrium lanuginosum* (Figure 14) and *Andreaea rupestris* (Figure 15) as well as *Racomitrium crispulum* (Figure 16) and *Rhacocarpus purpurascens* (Figure 17) from southern latitudes. Mires typically have *Calliergonella cuspidata* (Figure 18), and *Scorpidium scorpioides* (Figure 19), whereas less boggy ground may have *Pleurozium schreberi* (Figure 20). Tropical roadsides often have *Schistochilopsis incisa* and *Solenostoma sphaerocarpum*. On periodically submerged rocks one can find the ubiquitous *Platyhypnidium riparioides* (Figure 21), *Brachythecium plumosum* (Figure 22), and *Schistidium rivulare* (Figure 23), along with the southern latitude *Clasmatocolea vermicularis* (Figure 24) and *Cryptochila grandiflora* (Figure 25).



Figure 9. *Diplophyllum obtusatum*, a species that occurs in the tropics as well as at higher latitudes, but with a different habitat. Photo by Paul Davison, with permission.



Figure 10. *Solenostoma sphaerocarpa*, a species that occurs in the tropics as well as at higher latitudes, but with a different habitat. Photo by Michael Lüth, with permission.



Figure 11. *Schistochilopsis incisa*, a species that occurs in the tropics as well as at higher latitudes, but with a different habitat. Photo by Michael Lüth, with permission.



Figure 12. *Sphagnum magellanicum*, a species that occurs in the tropics as well as at higher latitudes, in bogs and poor fens. Photo by Michael Lüth, with permission.



Figure 13. *Sphagnum cuspidatum*, a species that occurs in the tropics as well as at higher latitudes, in bogs and poor fens. Photo by Michael Lüth, with permission.



Figure 14. *Racomitrium lanuginosum*, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Janice Glime.



Figure 15. *Andreaea rupestris*, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Michael Lüth, with permission.



Figure 16. *Racomitrium crispulum*, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Jan-Peter Frahm, with permission.



Figure 17. *Rhacocarpus purpurascens*, a species that occurs on rock outcrops in both latitudinal extremes, as well as the tropics. Photo by Michael Lüth, with permission.



Figure 20. *Pleurozium schreberi*, a typical mire species that occurs at high latitudes as well as the tropics and elsewhere. Photo by Janice Glime.



Figure 18. *Calliergonella cuspidata*, a typical mire species that occurs at high latitudes as well as the tropics. Photo by Des Callaghan, with permission.



Figure 21. *Platyhypnidium riparioides*, a rock-dwelling species that is periodically submerged in both high latitudes and the tropics. Photo by Michael Lüth, with permission.



Figure 19. *Scorpidium scorpioides*, a typical mire species that occurs at high latitudes as well as the tropics. Photo by Janice Glime.



Figure 22. *Brachythecium plumosum*, a rock-dwelling species that is periodically submerged in both high latitudes and the tropics. Photo by Michael Lüth, with permission.



Figure 23. *Schistidium rivulare* with capsules, a rock-dwelling species that is periodically submerged in both high latitudes and the tropics. Photo by Michael Lüth, with permission.



Figure 24. *Clasmatocolea vermicularis*, a rock-dwelling species that is periodically submerged in both high southern latitudes and the tropics. Photo by John Engel, through Creative Commons.



Figure 25. *Cryptochila grandiflora*, a rock-dwelling species that is periodically submerged in both high southern latitudes and the tropics. Photo by Felipe Osorio-Zúñiga, with permission.

Ah-Peng *et al.* (2007) demonstrated altitudinal gradients in bryophyte diversity on a 19-year-old lava flow in La Réunion. Because the lava flow is a uniform substrate, it provides an ideal opportunity for studying altitudinal effects without interference by substrate differences. Using quadrats in the range of 250-850 m asl, they determined that diversity increases with altitude, a pattern that occurs in many studies cited in this chapter. Nevertheless, a variety of available host plants seems to be important in fostering diversity (70 species) of epiphytic bryophytes on the lava flow.

In the Andes of Peru and Colombia, Kessler (2000) found floristically discrete communities that corresponded with altitudinal belts. He found that the floristic boundaries related to strong changes in **orography** (topographic relief of hills and mountains). These included the transition from the hilly lowland to the steep mountains, a co-occurring change in geological substrate at 400 m, a strong humidity gradient at 1,000 m on the Bolivian transect and at 1,250-1,980 on the Colombian transect, and the transition from mixed cloud forests to forests dominated by *Polylepis* (**Rosaceae**; Figure 26) or *Podocarpus* (a broad-leaved evergreen conifer; Figure 27). In relatively species-poor forest communities, the presence or absence of a few tree species influences the whole ecosystem. By contrast, in species-rich communities such as the forests at low to mid elevations, the elevational belts are ill-defined.



Figure 26. *Polylepis tarapacana*, a dominant tree in the cloud forest in Colombia. Photo by Rodrisan, through Creative Commons.



Figure 27. *Podocarpus*, a broad-leaved evergreen conifer in the mixed cloud forests of Colombia. Photo by Koppchen, through Creative Commons.

In 2017, von Konrat stated that his study of elevational bryophyte communities in the Fiji Islands was the first of its kind for Fiji. Von Konrat assessed presence/absence on the lower stems of the *Calophyllum* spp. (Figure 28) trees and on tree ferns at three elevations (~160 m, 590 m, and 1,260 m). Unlike the Uganda study of Tusiime *et al.* (2007 – see below), this one revealed a hump-shaped diversity distribution (Figure 7), with the greatest species richness in the mid elevation or upland forest. Liverworts dominated at all three elevations. The bryophyte communities were distinctly different at both the host tree level and among the three elevations.



Figure 28. *Calophyllum brasiliense*, a bryophyte host in the Fiji Islands. Photo by Mauro Halpern, through public domain.

Churchill *et al.* (1995) reported a moss diversity for the tropical Andes of 2,058 species comprised of 343 genera and 75 families. However, they considered that once the systematics are understood, and superfluous species are reduced to synonymy, this number is likely to drop to 1,500-1,700. The tropical Andes have a moss flora that is approximately eight times as rich in species as that of the Amazon basin. While α diversity (site diversity) may be similar, β diversity (differences in species composition among sites) and γ diversity (landscape diversity) in the Andes are much greater. These differences are largely due to **orographic** factors (relating to mountains, especially regarding position and form) (see also Pócs 1976). Nevertheless, the mosses do not seem to follow the latitudinal species gradient shown by other species groups. That is, there is no increase in number of species from the poles to the equator.

Despite these high numbers, one habitat had typically been overlooked in the early studies: the canopy. Particularly in the lowland rainforest, the canopy (Figure 29) houses a rich diversity with many species that are unique to the high canopy (Gradstein *et al.* 1990). In fact, these canopies can house more than 50% of the local species, as discussed in the sub-chapter on epiphytes.



Figure 29. Lowland rainforest tree, Colombian Amazon. Photo by Laura Campos, through Robbert Gradstein.

Campylopus pilifer (Figure 30) is broadly distributed and drought-tolerant and is found at high elevations in the tropics (Gradstein & Sipman 1978; Stech & Wagner 2005).



Figure 30. *Campylopus pilifer* (Dicranaceae), a broadly distributed species that occurs at high elevations in the tropics. Photo by Michael Lüth, with permission.

Westerners tend to think of Africa as the land of elephants and camels. But Africa has a remarkable topography and wide diversity of habitats. Tusiime *et al.* (2007) compared species richness among the habitats along an altitudinal range as well as along streamsides and trails in the forests of Bwindi Impenetrable National Park,

Uganda, using 1000-m transects with 1x1 m quadrats at 50 m intervals. In contrast with some of the Neotropical studies, richness of bryophyte species was negatively correlated with altitude. The exception to this was the thalloid liverworts, which increased with altitude. Streamside diversity was the highest, compared to that along trails. The evergreen forest had the greatest bryophyte richness, followed by the mature mixed and bamboo forests.

Additional studies discuss the effects of altitude on the bryophyte vegetation. Hedberg (1951) examined bryophytes in vegetation belts in the East African mountains and Pócs (1984) on Kilimanjaro. Bryant *et al.* (1973) demonstrated habitat differences among liverworts in ten areas of the Luquillo Mountains of Puerto Rico. Van Reenen and Gradstein (1983, 1984) investigated distribution and ecology on an altitudinal gradient in the Andes and on the Sierra Nevada de Santa Marta of Colombia; van Reenen (1987) reported on altitudinal zonation. Wolf (1989) reported on abundance of epiphytic communities along an altitudinal transect in the Cordillera Central, Colombia.

In some cases, soils may play a role in determining differences in bryophyte communities. Grieve *et al.* (1990) compared soils in six primary forest plots at 100 m, 500 m, 1,000 m, 1,500 m, 2,000 m, and 2,600 m asl on Volcán Barva, Costa Rica. As altitude increased, there was less evidence of intensity of weathering and organic matter decomposition. Simultaneously, subsoil clay content decreased from 80% at 100 m to less than 10% at 2000 m. Other soil factors likewise changed, with the ratio of free to total iron decreasing while surface organic matter increased. In fact, most nutrients at high elevations did not seem to be less than at low elevations.

On Mt. Kinabalu and the Himalaya of Bhutan, Ashton (2003) considered the floristic relationships to be complicated. He observed that the altitudinal level at which changes occur has only minor differences between the Equator and the tropical area. Rather, Ashton concluded that soil changes may play a more direct and important role than previously considered. The important soil factors are the increase in organic content in lower montane soils when compared to those of the lowland. This is accompanied by a change from termite-dominance to earthworm-dominance and frequency of dense moss layers and mor humus in the upper montane soils. But the question remains, do these soil differences make any differences in the composition of bryophyte communities?

Defining Zones

Enroth (1990) recognized five altitudinal zones in Papua New Guinea: 0-300 m, 300-1,200 m, 1,200-2,200(-2,300) m, 2,200(-2,300)-2,800(-2,900) m, and 2,800(-2,900)-3400 m asl. These zones are recognized by their distinct changes in the bryophyte flora. These zones also correspond well with previous studies on seed-plant flora. At the highest altitudes, species from the Northern Hemisphere occur. The high altitudes generally have New Guinean or Western Melanesian and Malesian endemics. At low to moderate altitudes, the flora is representative of Asian-Oceanian and Asian-Oceanian-Australian taxa, particularly among the mosses. Cosmopolitan species have either wide vertical ranges or occur only at high altitudes.

Van Reenen and Gradstein (1983) recognized five altitudinal bryophyte zones in the Sierra Nevadas of Colombia in the range of 500-4,100 m asl. Four zones are forest zones and one is **páramo** (high treeless plateau). They based their classification of these zones on relevés that included species presence, substrate preference, and percentage cover of bryophytes. The zones are correlated with precipitation and air temperature. Species presence and percent cover seem to be of equal importance in distinguishing the bryophyte zones in the forests. These are highest in the **condensation zones** (zones where water vapor in atmosphere condenses and becomes liquid).

Frahm and Gradstein (1991) examined the cover, biomass, and turnover rates of bryophytes in rainforests of Colombia, Peru, Borneo, and Papua New Guinea. From these, they concluded that altitudinal zonation is similar in different parts of the humid tropics.

In Hawaii, Kitayama and Mueller-Dombois (1992) studied the community organization on the windward slope of Haleakala. On a transect from 350 m asl to the summit at 3,055 m asl they used a Braun-Blanquet approach to record species. They found hierarchical arrangements that were correlated with altitude. The low to mid-altitudinal climate is wet, changing abruptly to an arid high-altitude climate. This climatic distinction created three broad zones with altitude: lowland, montane, and high-altitude zones. Further distinctions partitioned these into seven plant communities, six based on altitude and one dieback zone.

Zone Limitations

In Ecuador, the montane and lowland rainforests both have a cooler, wetter season from April to July (Grubb & Whitmore 1966). The montane site has fog-bound and fog-free days. On the fog-free days, sunshine may be present for a prolonged period. These sunny periods are longest in the dry season, lasting 1-2 weeks. On fog-bound days, there is little diel (within a period of 24 hours) temperature change and the relative humidity typically remains at 95% or higher. On fog-free days, the temperature range and minimum relative humidity are similar to those on an average day in the lowland forest. These fog conditions are absent in the lowland rainforest. Nevertheless, on the fog-bound days in the montane forests, the conditions are similar to those of the lowland forests in the wet season. The forest types correlate with the frequency of fog, not the temperature regime. The success and greater abundance of epiphytes in the montane forest compared to the lowland forest seems to result from the frequency of wetting by fog, not to a constantly higher humidity.

On a worldwide basis, Ashton (2003) is right; the causes of zonation with altitude are complicated. In Costa Rica, Kluge *et al.* (2006) studied the pteridophyte richness at 10-2800 m asl and at 2,700-3,400 m on the Atlantic slope of Costa Rica. They analyzed species richness in 156 plots of 20x20 m. They regressed species richness against temperature, humidity, precipitation, and actual evapotranspiration. As in many other studies, the species richness distribution of the 484 species was a hump-shaped one (Figure 7) typical of many elevational distributions in the tropics. And as is typical, it peaked at the mid-elevations. Nonetheless, the distribution correlated with the climatic variables of humidity and temperature. The mid-altitudes have the highest humidity and offer moderate

temperatures; high elevations have a reduced richness that the researchers attribute to the low temperatures. At low elevations, reduced water availability, coupled with high temperatures, reduce the species richness.

Low altitude bryophytes are limited by high temperatures and low light intensity (Richards 1984a; Frahm 1990a). In fact, the light intensity barely exceeds the **light compensation point** (intensity at which CO₂ lost by respiration = that fixed by photosynthesis). By contrast, montane bryophytes experience low temperatures and higher light intensities, with nearly horizontal rainfall and constant humidity, providing "suitable" conditions for a rich bryophyte flora (Pócs 1982; Richards 1984a; Stadtmüller 1987). The characteristics of the host plant for the predominantly epiphytic flora seem to be of minor importance.

Traditional assumptions have been that temperature, light intensity, and water availability determine the distribution of tropical bryophytes. Chantanaorrapint (2010) determined that in a slightly disturbed tropical forest in Thailand (Figure 31), it was a complex set of factors that affected the distributions of the epiphytic bryophytes. These related to these same altitudinal gradient factors of light intensity, air temperatures, and relative humidity working together.



Figure 31. Thailand rainforest. Photo courtesy of Och Nuchitprasitchai.

Kürschner (1995) demonstrated a strong correlation between known altitudinal zonation, forest zones, and plant sociological units in the tropics of the Democratic Republic of Congo and Rwanda (Figure 32). Because of their broad geographic distribution, relatively small number of species (compared to seed plants), sensitivity to climate, and prominence in tropical rainforests, bryophytes are good indicators of the altitudinal zonation pattern that is characteristic of the humid tropics.

There are a number of changes in the environment from lowland to montane, and these may work in consort, as noted by Chantanaorrapint (2010), to provide more favorable habitats in the mountains. Richards (1984b) suggested that lowland temperatures are too hot for most bryophytes. We can expect that these C₃ plants generally have their photosynthetic optimum around 20°C; mean annual temperatures in the montane rainforests are generally 10-20°C (Gradstein & Pócs 1989). As already

noted, Frahm (1990b) found that the rate of net assimilation of tropical montane bryophytes decreases radically above 25°C. Biebl (1964) showed that most of the bryophytes of the montane forest at El Yunque, Puerto Rico, could not survive at temperatures above 35°C. Light intensity in the lowlands is low, respiration (including photorespiration) is high, and moisture is often limiting, making it difficult for lowland bryophytes to assimilate more by photosynthesis than they lose to respiration. In fact, Frahm (1987) experimented in the laboratory with montane rainforest bryophytes from Peru and demonstrated just that – they cannot photosynthesize enough under the conditions of the tropical lowland rainforest. In such lowlands, one is most likely to find pantropical families such as **Calymperaceae** (Figure 134), **Hookeriaceae** (Figure 33), and **Lejeuneaceae** (Figure 76-Figure 94) (Gradstein & Pócs 1989).



Figure 32. Mount Miken, DR Congo, and Mount Karisimbi, Rwanda. Photo by Abel Kavanagh, through Creative Commons.



Figure 33. *Hookeria acutifolia* (Hookeriaceae); Hookeriaceae is a pantropical family found in Peruvian lowlands. Photo by John Game, through Creative Commons.

These dry conditions of the lowlands, however, do not persist throughout the other climatic zones of the tropics. In the lower montane rainforest in Panama (Figure 34), the daily water content of liverwort thalli is pronounced, and both the low and the high water content place considerable

limitation on the CO_2 exchange (Zotz *et al.* 1997). However, between those values is a range where a net carbon gain is possible. Even so, half of the mean daytime carbon gain is lost during the night due to respiration at the relatively high temperatures. Enough carbon is stored and not subsequently released to account for a net annual gain of approximately 45% of the initial carbon content of the thallus.



Figure 34. Panamanian montane forests. Photo by S. B. Matherson, through Creative Commons.

Additional studies include those by Grubb (1974) on the factors that control the distribution of forest types on tropical mountains in Malesia. Frahm (1990c) examined the altitudinal zonation of bryophytes on Mt. Kinabalu, Malaysia.

Transplant Studies

Experimental studies are few, but can provide a clearer picture of altitudinal relationships. Stam *et al.* (2017) transplanted 558 pendent epiphytes in the Afromontane forests of Taita Hills, Kenya (Figure 35). Several of the four pendent mosses grew very well in the upper montane forest where it was cool and humid, more than doubling their biomass in the year of study. By contrast, all of the transplanted mosses performed poorly in the humidity, heat, and low light of the lower canopy in the dense lower montane forests.



Figure 35. Taita Mountains, Kenya. Photo by Ina96, through Creative Commons.

Latitude vs Altitude

Delgadillo and Cardenas (1989) found that the highlands in the Chiapas of Mexico have moss floras similar to those of temperate regions. Truly tropical taxa are mostly confined to the lowland moist sites. The Meso-American species and species with wide distributions are the most numerous in species.

Churchill (1991) suggested that latitude does not play a major role in distinguishing moss diversity from high to low latitudes in the temperate and tropical regions. Rather, in Colombia (Figure 36), bryophyte species richness increases with altitude up to treeline (Figure 37). It is on the high mountains that the tropical bryophytes reach their zenith in diversity. A similar curve is seen for Yunnan, China (Figure 38) (Song *et al.* 2015). The hump shape (Figure 37-Figure 38) is typical of the diversity distribution.



Figure 36. Páramo in Colombia, showing vegetation above treeline. Photo by Friedrich Kircher, through Creative Commons.

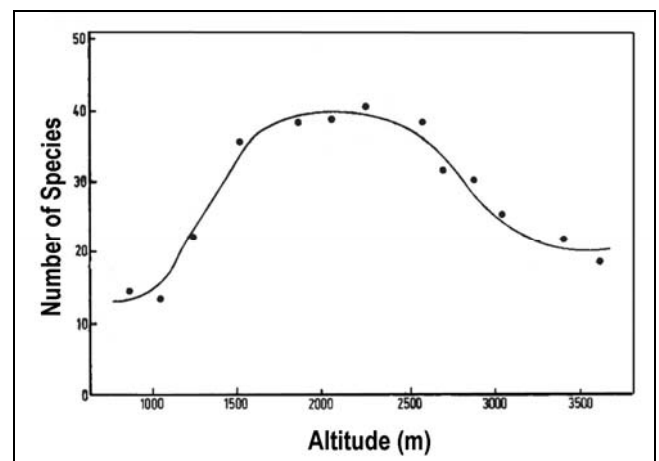


Figure 37. Species-altitude curve in Colombia. Modified from van Reenen & Gradstein 1983.

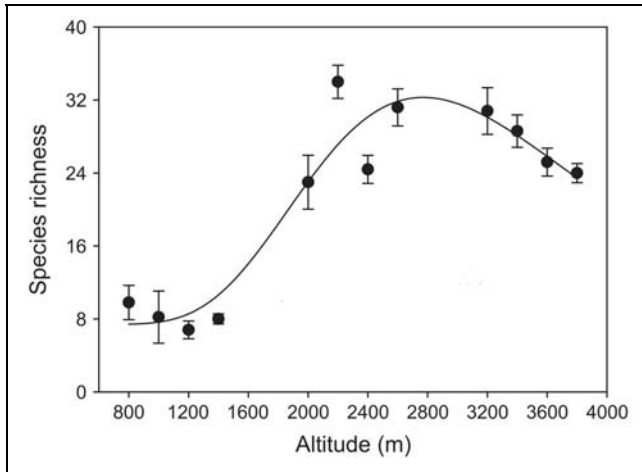


Figure 38. Mean (\pm SE) species richness for bryophytic epiphytes along altitudinal gradients in Yunnan, China. Modified from Song *et al.* 2015.

Churchill (1991) reported that ~93% of total species richness for mosses (900 spp.) in Colombia occurs within the 20-25% of land surface occupied by the Andes. Within that area, ~50% of diversity occurs at 2,600-3,300 m asl, the high montane zone. Among tropical bryophyte families, 60% are primarily montane while less than 5% are primarily lowland taxa. Freiberg and Freiberg (2000) also found higher bryophyte biomass in the montane zone of Ecuador (Figure 39) compared to the lowland forests, with a corresponding increase in dead organic matter. Similarly, in the Andes of Colombia (Figure 40), montane areas may produce at least ten times the epiphytic bryophyte biomass of lowland forests (van Reenen & Gradstein 1983). Frahm (1987) obtained similar biomass relationships in Peru (Figure 41). Lowlands and submontane regions also are deprived of endemics, sporting a number of transoceanic and pantropical taxa, especially liverworts in *Lejeuneaceae* (Figure 76-Figure 94) and mosses *Fissidens asplenioides* (Figure 42), *Floribundaria floribunda* (Figure 43), and *Neckeropsis disticha* (Figure 44), whereas endemics increase in number in alpine areas, causing the tropics to have a high number of endemic bryophytes (Gradstein *et al.* 2001a). Nöske *et al.* (2003) reported that in Ecuadorian Andes species range sizes decrease toward higher elevations, refuting **Rapoport's elevational rule** (prediction of trends of increased elevational ranges of plants with increase in elevation). It does suggest that more endemics might be expected at higher elevations. Nevertheless, endemism overall was very low (1%).



Figure 39. Alpine zone and snowline on Chimborazo volcano, Ecuadorian Andes. Photo by Bernard Gagnon, through Creative Commons.



Figure 40. Nevado del Ruiz, Andes, Colombia. Photo by Edgar, through Creative Commons.



Figure 41. Peruvian lowland forest. Photo by Irvin Calicut, through Creative Commons.



Figure 42. *Fissidens asplenioides*, a pantropical moss. Photo by David Tng, with permission.



Figure 43. *Floribundaria floribunda*, a pantropical moss. Photo through Creative Commons.



Figure 44. *Neckeropsis disticha*, a pantropical moss. Photo by Piers Majestyk, with permission.

Using only bole bryophytes to assess elevational differences eliminates most of the soil influences. Song *et*

al. (2015) compared bole bryophytes in three protected forest areas in tropical sub-montane (800-1400 m asl), montane (2000-2600 m asl) and sub-alpine (3200-3800 m asl) in Yunnan, SW China (Figure 45). They used 60 20x20 sampling plots, with five plots at each of 12 elevations with 200 m altitudinal intervals. They used 540 subplots, each with an area of 400 cm². These revealed 226 epiphytic bryophyte species. Life forms included smooth mat, fan, and turf as dominants in the sub-montane, montane, and sub-alpine forests, respectively (Figure 46). The sub-montane forest had significantly lower bryophyte species richness, a response they attributed to higher temperature, limited water availability, and more frequent human disturbance. As in many other studies cited here, the distribution of species richness was a hump-shaped curve with altitude (Figure 7), reaching its highest richness where the moisture levels were highest at ~2,600 m asl. Liverworts had the greatest species richness at all three sites (Figure 47).



Figure 45. Mountains at Yunnan, China. Photo by Ariel Steiner, through Creative Commons.

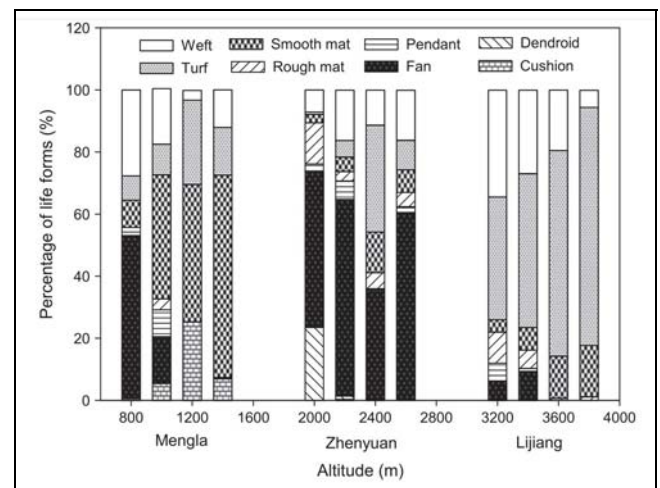


Figure 46. Comparison of life forms on three mountains in Yunnan, China. Modified from Song *et al.* 2015.

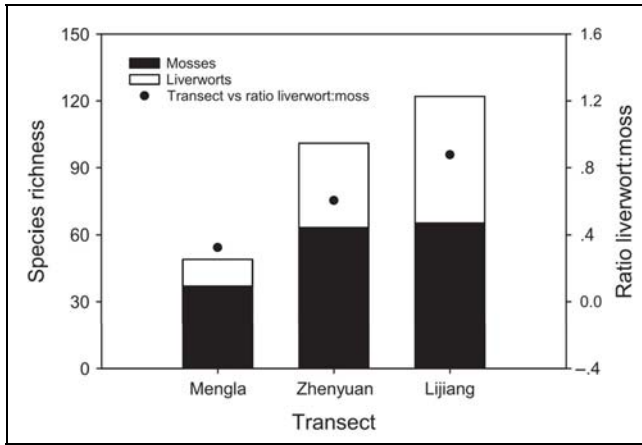


Figure 47. Species richness of mosses vs liverworts on three altitudinal transects in Yunnan, China. Species richness represents twenty 20 x 20 m plots on each mountain. Modified from Song *et al.* 2015.

Using data on more than 840 mosses and liverworts from the Himalayas in Nepal (actually subtropics; Figure 48), Grau *et al.* (2007) determined the known maximum and minimum elevations of the species. They found strong correlations in species richness among the ferns, flowering plants, mosses, and liverworts and elevational relationships. Maximum richness of liverworts occurred at 2,800 m, for mosses at 2,500 m asl. The endemic liverworts reached maximum richness at 3300 m; non-endemic liverworts at 2,700 m. Nevertheless, the mosses again did not support **Rapoport's elevational rule** (prediction of trends of increased elevational ranges of plants with increase in elevation). For liverworts, the relationship is not clear. Grau and coworkers (2007) suggest that differences in importance of climatic variables such as available energy and water might explain the differences among the four groups.



Figure 48. Himalaya Mountains at sunset, Nepal. Photo by Jules Air, through Creative Commons.

Records of Altitude

One might expect the highest known elevation for bryophytes to be in the tropics, where the climate will be the warmest at high elevations compared to the same elevation elsewhere. Grolle (1966) reported records up to 5100-5200 m asl in Nepal (subtropics). Alexey Potemkin (Bryonet 11 February 2016) noted that these were liverworts from a wide variety of genera: *Scapania*

ornithopodioides (Figure 49), *Lophozia incisa* (Figure 50), *Chandonanthus filiformis* (see Figure 51), *Gymnomitrium sinense* (see Figure 52), *Marsupella commutata* (Figure 53), *M. revoluta* (Figure 54), *Plagiochila carringtonii* subsp. *lobuchensis* (Figure 55), *Herbertus sendtneri* (Figure 56), *Anthelia julacea* (Figure 57), *Bazzania tricenata* (Figure 58), *Metacalypogeia alternifolia* (Figure 59).



Figure 49. *Scapania ornithopodioides*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 50. *Lophozia incisa*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 51. *Chandonanthus*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Blanka Agüero, with permission.



Figure 52. *Gymnomitrium concinnatum*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Hermann Schachner, through Creative Commons.



Figure 55. *Plagiochila carringtonii*, Scotland, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 53. *Marsupella commutata*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 56. *Herbertus sendtneri*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 54. *Marsupella revoluta*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 57. *Anthelia julacea*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 58. *Bazzania tricrenata*, a leafy liverwort that is among those at the highest elevations on the planet. Photo by Michael Lüth, with permission.



Figure 59. *Metacalypogeia alternifolia*, a leafy liverwort that is among those at the highest elevations on the planet. Photo through Creative Commons.

Schiavone and Suárez (2009) reported the moss *Globulinella halloyi* (Pottiaceae; see Figure 60) as a new species from Volcán Socompa, Argentina. It has the distinction of occurring at 6,000 m asl, 280-590 m higher than any known record for a bryophyte. It forms large, dense patches in communities with dense clumps of *Pohlia papillosa* (see Figure 63-Figure 64) on warm soil with moist conditions.

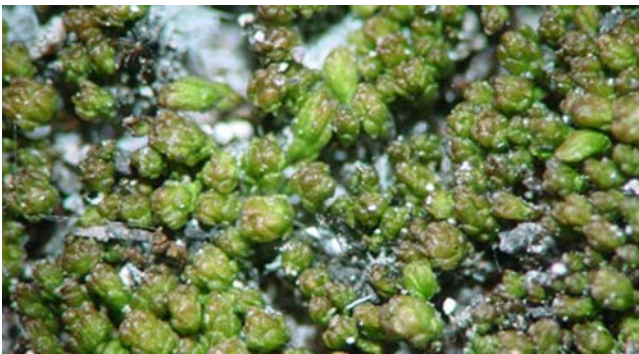


Figure 60. *Globulinella globulifera*; *G. halloyi* is a new species that occurs at 6000 m asl in Volcán Socompa, Argentina, making it the bryophyte at the highest elevation on the planet. Photo by Claudio Delgadillo Moya, with permission.

Volcanoes are particularly likely to have high-elevation bryophytes. Areas near geothermal vents have heated soil and sufficient moisture to maintain a suitable bryophyte habitat. Potemkin *et al.* (2018) reported two liverwort and two moss species from the top of Elbrus (5,590 m asl) in the Caucasus. They occupied an area free of snow and ice. The liverworts are *Marsupella boeckii* (see Figure 61) and *M. cf. funckii* (Figure 61). The mosses are *Atrichum cf. angustatum* (Figure 62) and *Pohlia nutans* (Figure 63-Figure 64), both widespread species. These are not tropical locations, and thus the high elevation is more remarkable, but the heat and moisture from the geothermal vent makes this habitat livable for these species. *Pohlia nutans* is also recorded from 3,000-4,000 m asl in China (Zhang *et al.* 2007). *Atrichum angustatum* is reported in Europe, Macaronesia, Turkey, Iran, eastern and central North America, and China. *Marsupella boeckii* is an infrequent Holarctic species; *M. funckii* is a European species.



Figure 61. *Marsupella funckii*, a species that occurs at 5,590 m asl in the Caucasus. Photo by Hermann Schachner, through Creative Commons.



Figure 62. *Atrichum angustatum* with ice crystals, a widespread species that occurs at 5,590 m asl in the Caucasus. Photo by Bob Klips, with permission.



Figure 63. *Pohlia nutans* below old mine on Svalbard. Photo by Michael Lüth, with permission.



Figure 64. *Pohlia nutans* in Khibiny Mountains, Apatity, Murmansk, a species that occurs at 5,590 m asl in the Caucasus. Photo by Michael Lüth, with permission.

Rodriguez (2015) reports the first known symbiosis in a high elevation (6480 m asl, Mt. Everest) population of mosses. The moss *Gymnostomum aeruginosum* (Figure 65) has a symbiotic fungus living completely within the tissues, making it the first documentation of a high elevation symbiosis. Rodriguez has continued testing to see if fungi confer any low temperature or high UV tolerance on the moss. Potemkin *et al.* (2018) have reported the Mt. Everest location of this species, based on a photograph, as hidden in a crevice in cold snow.



Figure 65. *Gymnostomum aeruginosum*, a moss with a symbiotic fungus at 6,480 m on Mt. Everest, possibly the highest elevation for a bryophyte. Photo by Hermann Schachner, through Wikipedia Commons.

Frey *et al.* (2012) listed the highest records for bryophytes in the Cordillera Real in Bolivia. The liverworts *Stephaniella paraphyllina* (Figure 66) and *Gymnocoleopsis multiflora* occur at 5,000 m asl. The moss *Grimmia longirostris* (Figure 67) occurs at 5,800 m asl. Thus it appears that the highest elevation record thus far goes to *Gymnostomum aeruginosum* on Mt. Everest.

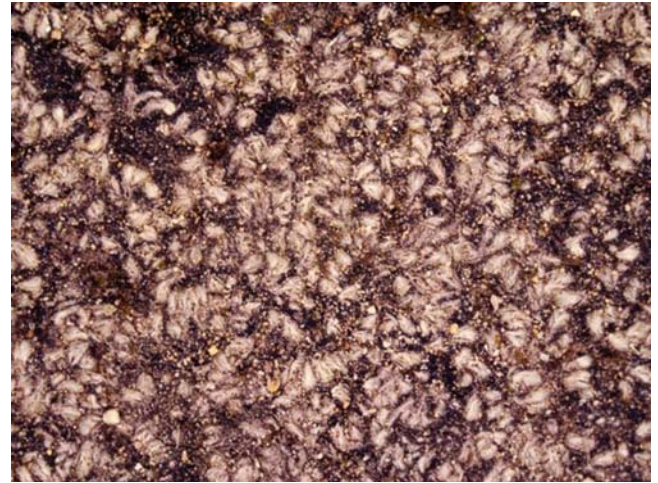


Figure 66. *Stephaniella paraphyllina*, a leafy liverwort species that occurs at 5,000 m asl in Bolivia. Photo by Jan-Peter Frahm, with permission.



Figure 67. *Grimmia longirostris* with capsules, a moss species that occurs at 5,800 m asl in Bolivia. Photo by Hermann Schachner, through Creative Commons.

Diversity-Richness Changes

Early studies recognized differences in the bands of vegetation as altitude increased. Bryologists naturally became curious about the co-occurring changes in the bryophyte vegetation.

Pócs (1984) used four transects on the SSW slope of Mt. Kilimanjaro to show bryophyte species changes in each 100-m altitudinal section. On this mountain they found that the number of species increased "rapidly" from 1,800 m asl upward. They found two peaks in species diversity, one at 2,200 m, where the structure of the montane rainforest is most complex, and one at 2,700 m in the cloud belt, where the precipitation is greatest. At timberline (3,000 m), there is a rapid decrease in species diversity, but this remains relatively constant until 3,800 m, where the vegetation is subalpine heath and it is more open and dry

with less rainfall. Above this level, the number of bryophyte species reach their minimum level on the mountain. The uppermost known species occurs at 5,050 m asl. These conditions created six bryophyte zones, each with characteristic species combinations, and these parallel the established zones of tracheophyte vegetation.

In Southwest Nigeria, Oyesiku (2013) conducted one of the rare ecological studies in a tropical rainforest biome in Africa. He found 138 bryophyte species, with 70% mosses and 30% liverworts. Unlike other studies, this one found the species distribution to be relatively homogeneous along the altitudinal trail (**Gini coefficient**=2.54%). A Gini coefficient of zero expresses perfect equality, where all values (species) are the same; 100% indicates that all values (species) are different. Nevertheless, there was a significant correlation between number of bryophyte species (for both mosses and liverworts separately) and elevation.

Frahm (1990c) investigated the altitudinal zonation of Bryophytes on Mt. Kinabalu in Borneo. Later, Frahm (1994a) summarized the results of the BRYOTROP Expedition to the Democratic Republic of Congo (previously Zaire) and Rwanda, which examined the altitudinal zonation of bryophytes on Mt. Kahuzi in the Democratic Republic of Congo. Based on bryophyte parameters such as species per hectare plot and altitudinal ranges of species, they identified four bryophyte vegetation zones: submontane forest (<1,500 m), lower tropical montane forest (1,500-2,000 m), upper tropical montane forest (2,100-2,800 m), and subalpine forest (2,900-3,200 m). These zones correlate with those previously named for the general tracheophyte vegetation.

Gradstein *et al.* (1983) compared liverworts between the Neotropics and Africa to determine the level of disjunction. Early researchers tended to name species on a new continent as new, but as more in-depth studies occur, many of these emerge as synonyms. Among 35 known Afro-American species, there are three distribution types one can recognize. These are Tropical Afro-American (lowland, montane, and the alpine element), Subtropical-Mediterranean (southern, wide element) and Temperate-SubAntarctic (southern, wide element). Most of these disjuncts occur in the leafy liverwort order **Jungermanniales** (Figure 10). The subtropical disjuncts are an exception, being thallose liverworts. The researchers suggest that the species disjunctions are due to long-distance dispersal, but experimental evidence to support this is totally lacking. On the other hand, it is possible that generic disjunctions and species vicariance might be the result of ancient land connections through Gondwanaland.

Although the bamboo forest (Figure 68) is low in bryophyte species diversity, it nevertheless exclusively hosted 17.6% of the collected bryophytes in the Bwindi Impenetrable National Park, Uganda (Tusiime *et al.* 2007).

Zhang (2001) demonstrated that the number of species per plot increases linearly with altitude in Hong Kong. Sun *et al.* (2013) found that the species richness of ground bryophytes on Gongga Mountain, China, shows no elevational trend. Cover, on the other hand, increases with elevation, with the maximum occurring at ~3,758 m asl,

with biomass averaging 700 g m⁻² and maximum thickness reaching 8 cm. For these ground dwellers, litter, air temperature, and precipitation seem to control distribution.



Figure 68. Uganda bamboo forest. Photo by A. M. Doughty, through Creative Commons.

Nekesa (2015) used a transect from 2,400 m to 4,800 m asl, sampling at 200-m intervals to examine the distribution of both bryophytes and tracheophytes on Mt. Kenya. Tracheophytes were sampled in 10 x 10 m quadrats with 10 x 5 cm bryophyte quadrats nested within them. Bryophytes had the highest diversity, followed by flowering plants. Diversity overall decreased from 2400 m asl to 460 m asl, with the optimum occurring at 2400 and 3000 m asl (over 350 species each). The most diverse bryophytes were humicolous and corticolous (80%) with only 0.001% in the aquatic habitat. Nekesa concluded that altitude is the major factor affecting the distribution of both groups, with microhabitats of bogs, rocks, and tracheophytes themselves being the secondary factors.

Glime *et al.* (1990) demonstrated a change in associations among **Frullania** (Figure 72) species with altitude on Mount Albert Edward, Papua New Guinea (Figure 69). The species diversity of this genus is greatest in the middle altitudes, least in the dry lowlands. Sibling taxa show elevational differences within pairs, thus occupying different niches. It is likely that we will find multiple environmental races among at least some species when we compare them among altitudes.



Figure 69. Mount Albert Edward, Papua New Guinea. Satellite image through Creative Commons.

On Mount Albert Edward, Papua New Guinea (Figure 69), there are more than 50 taxa of the leafy liverwort genus *Frullania* (Figure 72) (Glime *et al.* 1990). These taxa form many associations, often with other members of the same genus. The associations and the major taxa differ with elevation, and the species richness likewise differs. The most taxa occur at the middle altitudes, especially the cloud forests, and the least in the dry lowlands and high alpine areas. Furthermore, many clumps of single *Frullania* species occur in the latter two regions, whereas at the other elevations collections are rarely pure. In fact, at 2,000-2,500 m asl associations between *Frullania* taxa are so common between repeating species pairs or groups (*i.e.* high fidelity) that we (Glime *et al.* 1990) suggested that some benefit might be derived from the association. We suggested that these untested benefits might include:

1. high light intensity protection for small liverworts that live among larger ones in the forest canopy or in exposed alpine areas
2. protection from drying out by reducing the amount of free space among the branches and leaves
3. gain in water availability by species that have a poor ability to move water from the substrate or surface of the clump to their own branches but that can take advantage of the water moved by an associated species.

Although few authors describe such commensal water relationships in plants, except by use of mycorrhizae, Rydin (1985) has suggested that they exist among *Sphagnum* (Figure 70) species with differential abilities to absorb water in one circumstance and to retain it in another. His conclusions are further supported by the experimental studies of Li *et al.* (1992) on two additional species of *Sphagnum*.



Figure 70. *Sphagnum capillifolium* with capsules, in Chile. Photo by Juan Larrain, with permission.

Ah-Peng *et al.* (2012) compared altitudinal bryophyte species variation on the Reunion Island (summit 2,069 m asl) to that of the Colombia high volcano (5,321 m asl) on

the South American continent. Species richness was similar between the two locations, with 265 on Reunion Island and 295 on the Colombian volcano. On Reunion Island, species with small range sizes dominated, with mean altitudinal range increasing with altitude (perhaps Rapoport's elevational rule is right for bryophytes sometimes), and with species richness decreasing with altitude. The island's cloud forest has a high bryophyte species richness as well as a large number of rare species. The continental elevational gradient, by contrast, was dominated by large-ranged species.

The altitudinal gradient seems also to be reflected in the niche width (Figure 71) of the *Frullania* (Figure 72) taxa (Glime *et al.* 1990). At both the low and the high elevations, the niche widths are narrower (not supporting Rapoport's elevation rule), at least for the parameters tested, further restricting the taxa that are there to well-defined habitats. For example, *Frullania papillata* has 95% of its observations expected between 2,368 and 2,575 m asl and occurs only between 2,500 and 3,500 m. Similarly restricted taxa, altitudinally, include *F. apiculata*, *F. attenuata*, *F. gracilis* (Figure 72), *F. ornithocephala*, and *F. ornithocephala* var. *intermedia*. On the other hand, the middle altitudes have the highest number of species pairs with non-overlapping distributions (Figure 73).

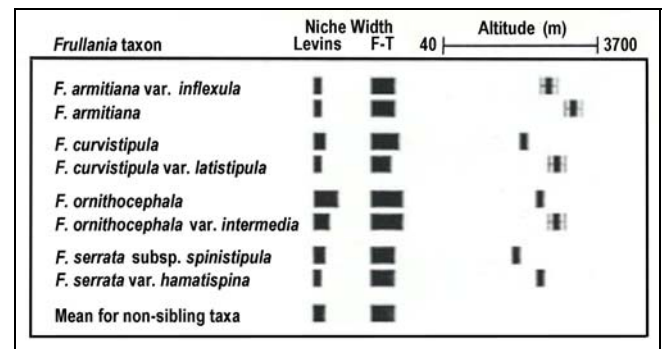


Figure 71. Levins and Freeman-Tukey niche width and elevational range of sibling pairs of *Frullania* on Mount Albert Edward, Papua New Guinea. Redrawn from Glime *et al.* 1990.



Figure 72. *Frullania gracilis*. Photo from Bryophyte Flora of Doi Suthep-Pui National Park, Chiang Mai, Thailand, through Creative Commons.

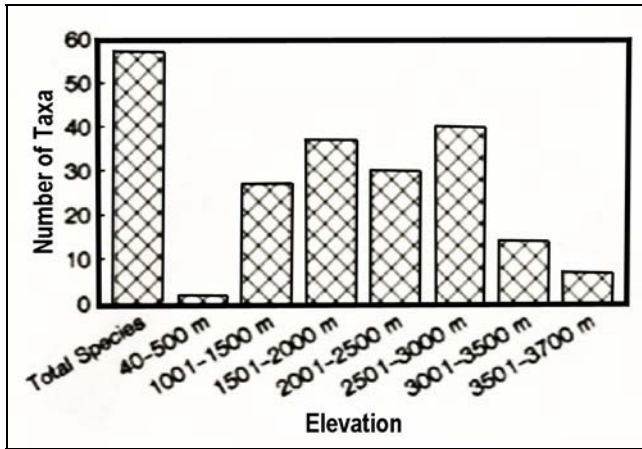


Figure 73. Elevational distribution of species richness of *Frullania* on Mount Albert Edward, Papua New Guinea. Redrawn from Glime *et al.* 1990.

Four sibling taxa pairs of *Frullania* occur (Figure 71, but among the ones examined, each member of the pair exhibits distinct altitudinal niches, suggesting that while they may have remained morphologically similar, they may have diverged physiologically (Glime *et al.* 1990).

The canopy typically has more species than the ground in a lowland rainforest. Cornelissen and Gradstein (1990), working in Guyana, reported that 50% of the species were restricted to the canopy; only 14% corticolous species were restricted to the understory. However, in Monteverde, Costa Rica (Figure 74), when rotten logs and living leaves are added to the understory percentage, about 20% of the species are exclusive to the understory (Figure 75) (Gradstein *et al.* 2001b). Gradstein and coworkers suggested that the percentage of species restricted to the canopy may be the same in lowland and montane rainforests, despite large differences in both species abundance and composition (see also Gradstein 1995).



Figure 74. Monteverde, Costa Rica, canopy. Photo by Cephas, through Creative Commons.

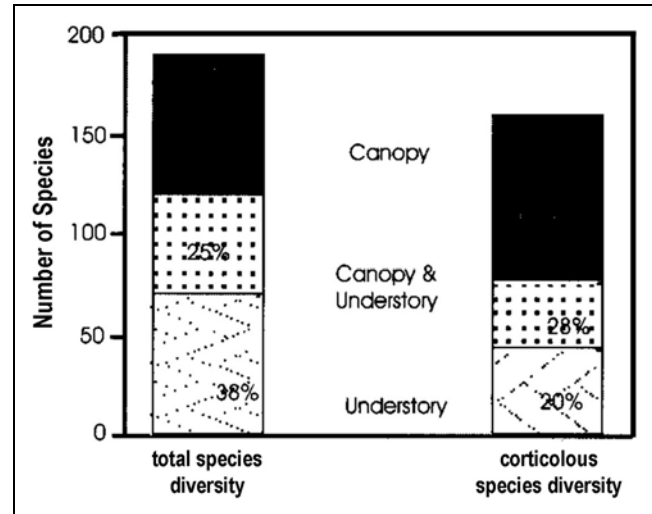


Figure 75. Diversity of canopy vs understory in the cloud forest at Monteverde, Costa Rica. Modified from Gradstein *et al.* 2001b.

Eggers (2001) described the groupings of epiphyllous *Lejeuneaceae* (Figure 76-Figure 94) in Costa Rica based on their altitudinal distribution:

only <500 m:

Cololejeunea setiloba (see Figure 77)

1-1,600 m:

Cololejeunea (syn.=*Aphanolejeunea*) *costaricensis* (see Figure 76), *Cololejeunea moralesiae* (see Figure 76), *Cololejeunea cardiocarpa* (Figure 77), *C. guadeloupensis* (see Figure 77), *C. linopteroides* (see Figure 77), *C. obliqua* (see Figure 77), *C. minutilobula* (see Figure 77), *C. standleyi* (see Figure 77), *Colura verdoornii* (see Figure 78), *Cyclolejeunea chitonia* (see Figure 79), *C. peruviana* (Figure 79), *Diplasiolejeunea brunnea* (Figure 80), *Microlejeunea epiphylla* (see Figure 81), *Rectolejeunea berteriana* (Figure 82), *R. cf. emarginuliflora* (see Figure 82), *Stictolejeunea squamata*.



Figure 76. *Cololejeunea microscopica*; *Cololejeunea costaricensis* and *C. moralesiae* occur from 1 to 1,600 m asl in Costa Rica. Photo by Stan Phillips, through public domain.



Figure 77. *Cololejeunea cardiocarpa*, a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Paul Davison, with permission.



Figure 80. *Diplasiolejeunea brunnea* in Ecuador on leaf, a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Tamás Pócs, with permission.



Figure 78. *Colura tenuicornis*; *C. verdoornii* is a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 81. *Microlejeunea* sp.; *M. epiphylla* is a leafy liverwort species that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Tangatawhenua, through Creative Commons.



Figure 79. *Cyclolejeunea peruviana*, a leafy liverwort species (as well as *C. chitonina*) that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Jan-Peter Frahm, with permission.

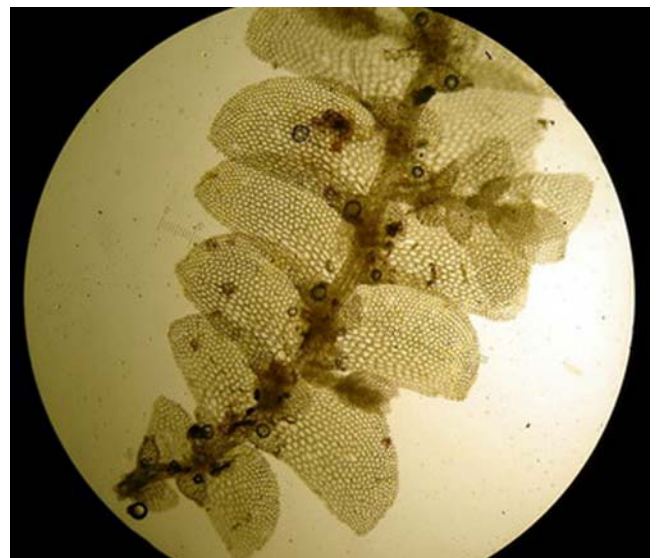


Figure 82. *Rectolejeunea berteriana*, a leafy liverwort species (as well as *R. cf. emarginuliflora*) that occurs from 1 to 1,600 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

1-3,000 m:

Cololejeunea (syn.=*Aphanolejeunea*) *angustissima* (see Figure 76), *Colura tortifolia* (Figure 83), *Diplasiolejeunea cavifolia* (Figure 80, Figure 84), *D. pellucida* (Figure 84), *Drepanolejeunea inchoata* (Figure 85), *Dr. lichenicola* (see Figure 85), *Lejeunea laetevirens* (Figure 86), *Odontolejeunea lunulata* (Figure 87).

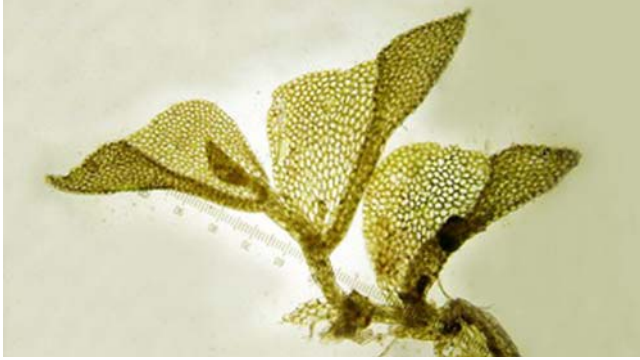


Figure 83. *Colura tortifolia*, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.



Figure 84. *Diplasiolejeunea pellucida*, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

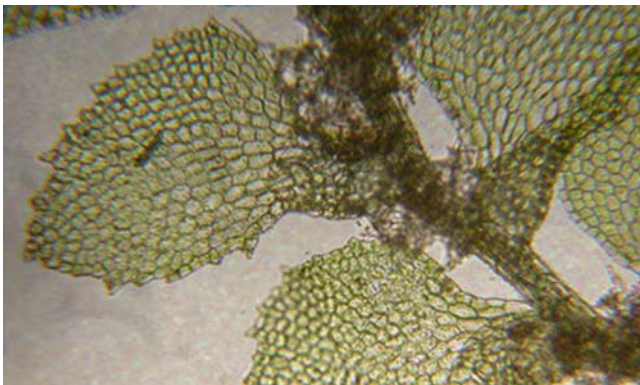


Figure 85. *Drepanolejeunea inchoata* (as well as *Dr. lichenicola*), a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.



Figure 86. *Lejeunea laetevirens*, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Scott Zona, through Creative Commons.



Figure 87. *Odontolejeunea lunulata* with perianth, a leafy liverwort species that occurs from 1 to 3,000 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

only 500-1,600 m:

Cololejeunea (syn.=*Aphanolejeunea*) *cingens* (see Figure 76), *Cololejeunea* (syn.=*Aphanolejeunea*) *longifolia* (Figure 88), *Cololejeunea* (syn.=*Aphanolejeunea*) *pustulosa* (see Figure 76), *Cyclolejeunea accedens* (see Figure 79), *C. convexistipa* (see Figure 79), *Diplasiolejeunea grolleana* (see Figure 80, Figure 84), *D. unidentata* (see Figure 80, Figure 84), *Harpalejeunea uncinata* (see Figure 89), *Lejeunea filipes* (Figure 90), *Odontolejeunea decemdentata* (Figure 91).



Figure 88. *Cololejeunea longifolia*, a species that occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Yang Jia-dong, through Creative Commons.

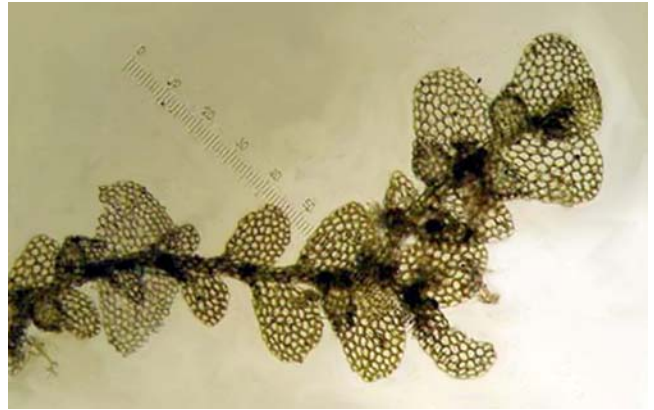


Figure 90. *Lejeunea filipes*, a leafy liverwort species that occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.



Figure 89. *Harpalejeunea latitrans*; *H. uncinata* occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Jeremy Rolfe, through Creative Commons.

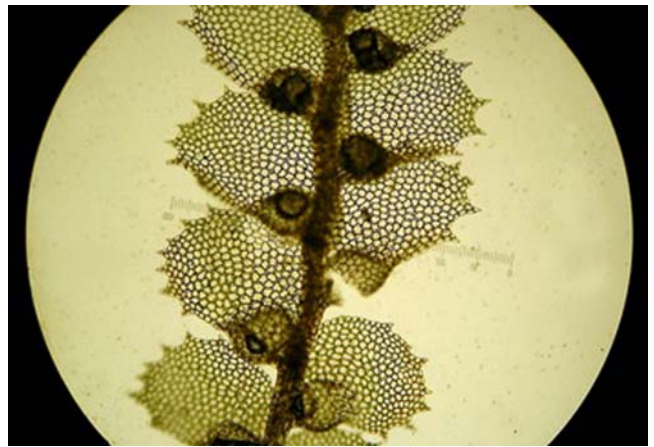


Figure 91. *Odontolejeunea decemdentata*, a leafy liverwort species that occurs only from 500 to 1,600 m asl in Costa Rica. Photo by Michaela Sonnleitner, with permission.

500-3,000 m:

Anoplolejeunea conferta, *Cololejeunea* (syn.=*Aphanolejeunea*) *crenata* (see Figure 76), *Cololejeunea* (syn.=*Aphanolejeunea*) *ephemeroides* (see Figure 76), *Colura tenuicornis* (Figure 78), *Diplasiolejeunea alata* (see Figure 80, Figure 84), *Drepanolejeunea infundibulata* (see Figure 85), *Dr. mosenii* (see Figure 85), *Lejeunea flava* (Figure 92- Figure 93), *Omphalanthus filiformis* (Figure 94).



Figure 92. *Lejeunea flava*, a leafy liverwort species that occurs from 500 to 3,000 m asl in Costa Rica. Photo by Linda Phillips, through Creative Commons.



Figure 93. *Lejeunea flava* on a leaf, a leafy liverwort species that occurs from 500 to 3,000 m asl in Costa Rica. Photo by Yang Jia-dong, through Creative Commons.



Figure 94. *Omphalanthus filiformis* in the Neotropics, a leafy liverwort species that occurs from 500 to 3,000 m asl in Costa Rica. Photo by Michael Lüth, with permission.

only >1,600-3,000 m:

Cololejeunea (syn.=*Aphanolejeunea*) *camillii* (see Figure 76), *Cololejeunea fefeana* (see Figure 77), *Diplasiolejeunea costaricensis* sp. nov. (see Figure 80, Figure 84), *D. involuta* (see Figure 80, Figure 84).

In Panama, Gradstein and Salazar Allen (1992) assessed the bryophytes along an altitudinal gradient on Cerro Pirre (1,200 m asl). As shown in the other studies above, they found very different species assemblages along the gradient from inundated lowland, to hillside lowland, to submontane, to montane elfin forest. Among these, they found the greatest species richness in the submontane forest. The greatest number of exclusive species, however, occurred in the montane elfin (cloud) forest, along with the greatest bryophyte biomass. The mountain proved to have a number of rare liverworts, and this one study produced 40 liverwort species new for Panama.

Wolf (1989, 1992) elaborated on the species richness of epiphytic bryophytes on an altitudinal gradient in the northern Andes (Figure 95). This study included 187 liverworts and 108 mosses. Wolf (1993a, b) also examined the diversity patterns and biomass of epiphytic bryophytes along this gradient in the Central Cordillera of Colombia

(Figure 96) from 1,000 to 4,130 m asl. Altitude emerged as a complex factor in explaining the variation in species composition. Species area curves for each sampling site indicated that sampling was adequate. α and β diversity patterns along the altitudinal gradient differed between mosses and liverworts. Liverwort richness was maximum (~100 taxa) in the range of 2,550-3,100 m. This high level corresponds with the contact transition zone between vegetation zones. This supports the prediction that the highest species diversity will occur in a transition zone, indicating that between community interactions are more important in determining diversity than within community relationships (*i.e.* niche relationships). This is further supported by the fact that only 20.5% of the liverwort taxa are exclusive to this belt of greatest richness. Humidity appears to be an important limiting factor, with biomass increase of bryophytes corresponding with a humidity increase with altitude. Bryophyte species turnover also appears to be greater in this mountain system than that known for the temperate mountains in North America.



Figure 95. Nevado del Ruiz, northern Andes, Colombia. Photo by Edgar, through Creative Commons.



Figure 96. Western Cordillera of Colombia bordering Chocó, very rich montane cloud forests on a sunny day at 1,600 m in 1992. Photo courtesy of S. Robbert Gradstein.

The ECOANDES project has contributed greatly to our understanding of Neotropical altitudinal effects on bryophytes (Gradstein *et al.* 1989). Gradstein and coworkers compared the wet, foggy western slope (1,000-4,500 m) with the drier eastern slope (500-4,500 m) of the Colombian Central Cordillera at the Parque de los

Nevados. Again, the species richness increases with altitude to the upper montane forest, where the greatest bryophyte diversity occurs. Liverworts demonstrate their greater preference for moisture by outnumbering mosses in the upper submontane and montane forests on the wet western slope, but in the drier environments they are less diverse than the mosses. At lower altitudes (<3000 m), the species are wide-ranging tropical species, whereas in the higher altitudes the species are those with narrow ranges (Andean and endemics). Few temperate species occur, with less than 10% in the upper montane forest and ~20% in the páramo. We can assume they have arrived in Colombia relatively recently (last 5 million years) after the Cordilleras arose.

Germano and Pôrto (2006) reported on bryophyte communities in the remnant Atlantic forests in Pernambuco, Brazil. In the Atlantic Forest of Rio de Janeiro, southeastern Brazil, Santos and Costa (2010) reported 360 liverwort taxa. In addition to having floristic differences among the different formations, there were altitudinal differences. The montane forest has the highest species richness (238) with 63 exclusive taxa and 27 endemics, as of the year 2010. The upper montane is next with 173 species, 58 exclusive taxa, and 21 endemics. The leafy liverwort family **Lejeuneaceae** (Figure 76-Figure 94) is the most species-rich family in all formations, whereas other families may be restricted to certain formations.

In the Itatiaia National Park (Figure 6) of Brazil, three vegetation zones are clearly defined: montane forest (Figure 97), upper montane forest (Figure 97), and high-altitude fields (Figure 98) (Costa *et al.* 2015). Sampling at 10 representative elevations revealed 519 taxa, 57% of the total known bryophyte flora in the Rio de Janeiro State and 34% of that of Brazil. The montane forest had the highest species richness (296). The most endemic species (47) occurred in the upper montane zone. The researchers attributed the richness in these locations to their diversity of climate, soil, and physiographic parameters. As is typical in the tropics, especially the Neotropics, the highest diversity occurs at the mid-altitudinal range of 2,100-2,200 m asl. As the altitude increases, so does the number of threatened species.



Figure 97. Montane and upper montane forests, Parque Nacional de Itatiaia, Brazil. Photo by Gabriel R. Vallim, through Creative Commons.



Figure 98. High-altitude field, Parque Nacional do Itatiaia, Rio de Janeiro, Brazil. Photo by Pedro Luz, through Creative Commons.

On Mt. Kitanglad (up to 2,938 m asl) in the Philippines (Figure 99), Azuelo *et al.* (2010) examined the diversity and ecology of bryophytes. They report 428 species, with mosses predominating. Of these, 326 species are mosses; only 98 of these species are liverworts and 4 are hornworts. The mosses occur in 70 genera and 29 families. The highest diversity occurs in the lower montane forest (112 species), followed by the mossy (cloud) forest (108 species) and upper montane forest (87 species). Nevertheless, the highest bryophyte cover occurs in the mossy forest. A major substrate choice is epiphytic (40% of mosses, 15% of liverworts, and 1 hornwort). But, the highest richness is on the rotten logs and decaying litter, with 43% of the mosses and 42% of the liverwort species occurring there, including **Lepidoziaceae** (Figure 100), **Plagiochilaceae** (Figure 55), **Schistochilaceae** (Figure 11), and **Trichocoleaceae** (Figure 101). The moss families **Meteoriaceae** (44 species; Figure 43) and **Dicranaceae** (43 species; Figure 30) are the most species-rich families, contrasting with the prominence of the liverwort family **Lejeuneaceae** (Figure 76-Figure 94) in most areas of the tropics. Rather, the **Plagiochilaceae** (26 species) and **Lepidoziaceae** (20 species) are the most species-rich liverwort families. Among the species on the mountain, 11 moss and 6 liverwort species are considered to be medicinal.



Figure 99. Mt. Kitanglad, Philippines. Photo by Kleomarlo, through public domain.

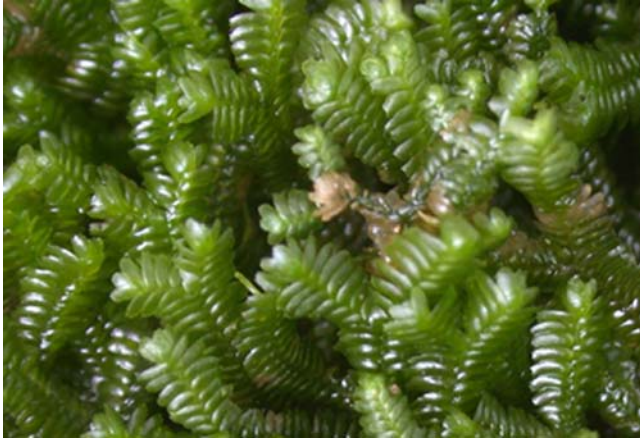


Figure 100. *Bazzania tridens*, in the family **Lepidoziaceae**, one of the common families of liverworts on logs and decaying matter in the Philippines. Photo by Li Zhang, with permission.



Figure 101. *Trichocolea tomentella*; **Trichocoleaceae** is a common family on rotten logs and decaying litter in the Philippines. Photo by Dick Haaksma, with permission.

Santos *et al.* (2017) compared the numbers of species in families at six altitudes at the Serra do Mar State Park, Brazil (Figure 102)

In an attempt to determine the usefulness of liverworts as bioindicators, Santos *et al.* (2014) sampled 26 localities to determine β diversity relationships. They found a significant association of the first CCA axis with a floristic gradient from lowland forests to high montane forests. They found 34 species that could serve as bioindicators. The species groupings could be explained by altitude, temperature, and precipitation.

Churchill (pers. comm. 29 November 2011) has observed that diversity relationships with altitude are basically true throughout the tropical Andes.

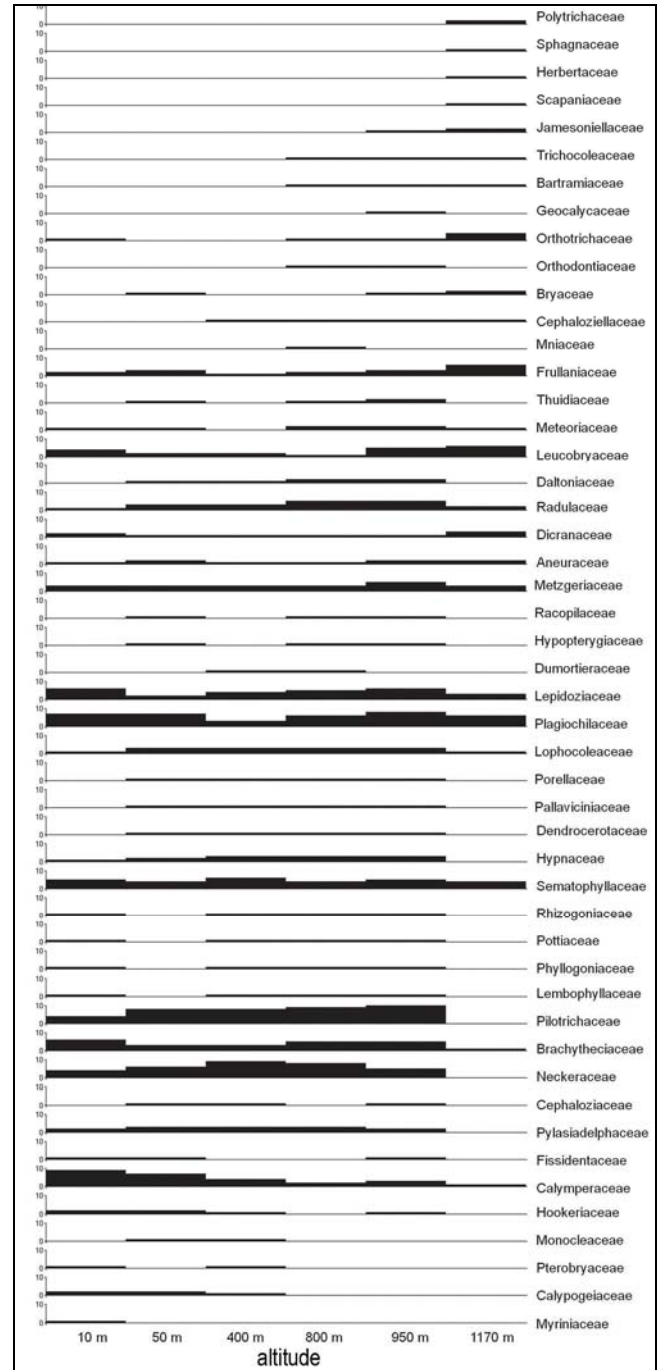


Figure 102. Abundance of species in families by elevation in Serra do Mar State Park, Brazil. Height of bar denotes number of species. **Lejeuneaceae** are not included. Modified from Santos *et al.* 2017.

Dominance Changes

As the elevation increases, the dominant species change. Santos *et al.* (2017) illustrated this clearly in the Atlantic Forest in Serra do Mar State Park, Brazil (Table 1).

Table 1. Indicator species of bryophytes with a p value ≤ 0.03 from five vegetation types in the Atlantic Forest in Serra do Mar State Park, Brazil, demonstrating the change in dominance with elevation.

RESTINGA FOREST

Bazzania phyllobola

Leptolejeunea elliptica

Cololejeunea obliqua

Syrrhopodon incompletus

Plagiochila disticha

Harpalejeunea oxyphylla

Figure 103

Figure 104

Figure 105

Figure 106

LOWLAND FOREST

Crossomitrium patrisiae

Figure 107

SUBMONTANE FOREST

Bryopteris filicina

Figure 108

Homalia glabella

Figure 109

Ceratolejeunea rubiginosa

Tortella sp.

Figure 110

Homaliodendron piniforme

MONTANE FOREST

Porotrichum longirostre

Radula nudicaulis

Racopilum tomentosum

Figure 111

Thamniopsis langsdorffii

Figure 112

Bazzania stolonifera

Figure 113

MOUNTAINTOP FOREST

Jamesoniella rubricaulis

Figure 114

Schlotheimia tecta

Figure 115

Cheilolejeunea xanthocarpa

Figure 116

Frullania atrata

Figure 117

Frullania kunzei

Figure 118

Campylopus heterostachys

Figure 119

Frullania apiculata

Herbertus juniperoideus subsp. *bivittatus*

Figure 120

Macromitrium cirrosum

Figure 121

Plagiochila bifaria

Figure 122

Campylopus griseus

Figure 123

Campylopus pilifer

Figure 30

Polytrichum juniperinum

Figure 124

Schlotheimia jamesonii



Figure 103. *Leptolejeunea elliptica*, an indicator species of the Restinga Forest. Photo by Yan Jia-dang through Creative Commons.



Figure 104. *Cololejeunea obliqua*, an indicator species of the Restinga Forest. Photo by Jan-Peter Frahm, with permission.



Figure 105. *Syrrhopodon incompletus* with capsules, an indicator species of the Restinga Forest. Photo by John Bradford, with permission.



Figure 106. *Plagiochila disticha*, an indicator species of the Restinga Forest. Photo by Michael Lüth, with permission.



Figure 109. *Homalia glabella*, an indicator species of the Submontane Forest. Photo by Claudio Delgadillo Moya, with permission.



Figure 107. *Crossomitrium patrisiae*, an indicator species of the Lowland Forest. Photo by Michael Lüth, with permission.



Figure 110. *Tortella humilis*, an indicator species of the Submontane Forest. Photo by Michael Lüth, with permission.



Figure 108. *Bryopteris filicina*, an indicator species of the Submontane Forest. Photo by Michael Lüth, with permission.



Figure 111. *Racopilum tomentosum*, an indicator species of the Montane Forest. Photo by Michael Lüth, with permission.



Figure 112. *Thamniopsis langsdorffii*, an indicator species of the Montane Forest. Photo by Michael Lüth, with permission.



Figure 115. *Schlotheimia tecta*, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.



Figure 113. *Bazzania stolonifera*, an indicator species of the Montane Forest. Photo by Michael Lüth, with permission.



Figure 116. *Cheilolejeunea xanthocarpa*, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.



Figure 114. *Jamesoniella rubricaulis*, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.



Figure 117. *Frullania atrata*, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.



Figure 118. *Frullania kunzei*, an indicator species of the Mountaintop Forest. Photo by Blanka Aguero, with permission.



Figure 121. *Macromitrium cirrosum*, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.



Figure 119. *Campylopus heterostachys*, an indicator species of the Mountaintop Forest. Photo by Germaine Parada, through Creative Commons.



Figure 122. *Plagiochila bifaria*, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.



Figure 120. *Herbertus juniperoides*, an indicator species of the Mountaintop Forest. Photo by Jan-Peter Frahm, with permission.



Figure 123. *Campylopus griseus*, an indicator species of the Mountaintop Forest. Photo by Michael Lüth, with permission.



Figure 124. *Polytrichum juniperinum*, an indicator species of the Mountaintop Forest. Photo by Janice Glime.

Productivity

Zotz (1999) found a distinct increase in abundance of mosses and liverworts with altitude. They are especially important in tree crowns in montane regions and are inconspicuous in the lowlands. This study demonstrates that drying in the daytime in the lowlands limits photosynthesis, whereas hot, moist nights cause excessive respiration that exceeds photosynthetic gain.

Based on studies in Borneo, Tanzania, Transvaal, Venezuela, and Peru, Frahm (1990b) concluded that the biomass of epiphytic bryophytes in the tropics increases from the lowlands to the **treeline** (altitude above which trees cannot grow). Like the conclusions of Zotz (1999), he attributed this gradient to combinations of precipitation, humidity, temperature, and desiccation. This was supported by experiments showing that net assimilation decreases rapidly above 25°C. The high temperatures and low light result in higher respiratory losses compared to photosynthetic gains. This problem is further exacerbated by problems of desiccation in lowlands. At higher altitudes, on the other hand, the abundant precipitation carrying a relatively high nutrient supply enhances growth in the tropical montane forests.

In this study, Frahm (1990b) compared the monthly and yearly production and chlorophyll content of the perennial moss *Hydrogonium* (Figure 125) and the seasonal moss *Physcomitrium* (Figure 126) and their associated communities in 10 x 10 cm quadrats. For *Hydrogonium*, the mean biomass was 95 g m⁻² and for *Physcomitrium* 11 g m⁻². These values are both lower than many measures of bryophytic biomass in temperate forests.

Bader *et al.* (2013) found a similar increase in biomass from lowlands to highlands in Panama, with increases to "extreme richness" in some montane cloud forests. Using gas-exchange measurements before and after transplanting bryophytes to lower altitudes, these researchers determined that temperature alone could not explain the lack of success of high altitude species in the lowlands. Nevertheless, a few samples of nearly every species survived for at least 20 months. Hydration patterns proved to be important in the survival. Sunny mornings cause rapid desiccation, a regime that can be deadly to many species. This is further complicated by afternoon rains that hydrate the mosses,

renewing their activity and causing high respiratory losses at night.



Figure 125. *Hydrogonium ehrenbergii*; in the tropics this genus has lower biomass than in the temperate zone. Photo by Jan-Peter Frahm, with permission.



Figure 126. *Physcomitrium eurystomum*; the genus *Physcomitrium* in the tropics seems to have lower productivity than populations in the temperate zone. Photo by Show-Ryu, through Creative Commons.

Wagner *et al.* (2012) noted that **poikilohydric** organisms (those with predominantly external control over water content, including bryophytes) increase with altitude in the tropics. In the lowlands, low light and high temperatures cause a high respiration to photosynthesis ratio, often causing bryophytes to have negative net productivity. Among 18 tropical bryophytes in the study, from three altitudes (sea level, 500 m, 1,200 m) in Panama, the optimum temperatures of net photosynthesis closely matched the mean temperatures of the habitats where the species grew. This adaptation resulted in a lack of differences in the ratio of dark respiration to net photosynthesis with altitude. As one might surmise from this, responses of individual species to water, light, and CO₂ did differ, but not systematically with altitude. Water relations seemed to be important, with higher temperatures increasing the evaporation rates. This, in turn, decreased the time available for photosynthesis each day, while nighttime respiration rates did not necessarily increase.

Chantanaorrapint (2010) compared biomass of epiphytes along three altitudinal transects in southern

Thailand, ranging from 25 m asl to 1,500 m asl. The dry weight of epiphytic bryophytes increased with altitude, with 1.15 g m^{-2} in the lowland to 199 g m^{-2} in the montane forests. The dry weight increased with altitude from 2.4 kg per hectare to 620 kg per hectare. These bryophytes were important in water storage, holding 1.2 to 2.4 times their dry weight. This storage was typically higher in the montane region (up to $1,500 \text{ L ha}^{-1}$) than in the lowland forests. Bark pH also varies with altitude, ranging from 3.19 to 6.84, decreasing with altitude. Air temperature decreases about 0.6°C per 100 m increase in elevation.

Zotz *et al.* (1997) measured CO_2 exchange in six tropical bryophytes in a lower montane forest in Panama. The **diel** water content varied greatly. Both low and high water content were severely limiting for photosynthesis. Low photon flux density (a measure of light intensity), as occurs during rain storms, was less limiting for CO_2 exchange than water availability. More than half of the daily carbon gain of 2.9 mg C g^{-1} was lost at night to respiration. This suggests an estimate of 45% carbon gain for the bryophytes per year.

Adaptations

There appear to be distinct adaptations that characterize forest epiphytes in altitudinal zones throughout the tropical regions of Southeast Asia, Africa, and South America (Kürschner *et al.* 1999). In the tropical lowlands and submontane regions, **perennial stayer** and **perennial shuttle species** dominate the life forms. In the cooler and more humid montane rainforests, **fan** and **weft** forms of **perennial stayers** and **perennial shuttle** species are prominent, relying on propagules and clonal growth to achieve the large biomass found there. These **fan**-forms and other structures such as ciliate leaves are effective at trapping fog water through rapid condensation and facilitating conduction and storage. In the upper montane forests, conditions are more open and xeric and the diurnal fluctuations are more extreme. Here the bryophytes tend to form **cushions** or **short and tall turfs** of **perennial stayers** and **perennial shuttle** species. They often conserve water through an abundant rhizoid tomentum and a more developed central strand in the stem.

Frahm (1994b), as part of the BRYOTROP Expedition, reported on life forms from various elevations on Mt. Kahuzi (Democratic Republic of the Congo), using a transect from 900 to 3,300 m asl. From 900 to 2,300 m elevation, the **dendroid** life form is characteristic. He interprets this as an adaptation for better gas exchange in conditions of low light and high air humidity. **Cushions** predominate above 2,500 m asl. These are typically 2-5 cm high, but some reach 50 cm at treeline. **Moss balls** can form, reaching up to 1 m in diameter. Bryophyte cover on soil is less than 5% below 2,700 m asl, but in the subalpine ericaceous belt it is 90%. Similarly, cover on bark is as low as 5% or less in the low elevations, increasing to 80% at high elevations. This gradation corresponds with light intensities from <1% to up to 50%. Temperature, on the other hand, decreases from 10.6°C at 900 m to 1.5°C at 4,500 m. The bark pH is in a relatively narrow range of 4.1-6.2.

In the Amazonian Andes in northern Peru (Figure 127), Kürschner and Parolly (1998a, b) were able to define apparent adaptations based on relative biomass of

morphological types. They found three dominant life strategy categories: **colonists**, **perennial shuttle species**, and **perennial stayers**. However, the **colonists** were confined to disturbed sites and were not typical of the elevational zones. Lowland bryophytes exhibit **mat** forms with water lobules, water sacs, and rhizoid discs. The balance of high temperatures with the humidity of both the lowlands and submontane belt seem to favor the passive reproduction (having low or moderately low sexual and asexual reproduction) of **perennial shuttle** and **perennial stayer species**. In the more humid and often foggy montane zone, the **mat** forms of the lowlands disappear and **dendroid** and **pendent** forms join the more universal **fan** and **weft** forms – all forms that are able to condense water from the fog and mist (**fog-stripping**). The leaves are often ciliate or deeply fissured and frequently have a **rill-like** arrangement (like series of small, narrow valleys), all characteristics that facilitate water uptake, conduction, and storage. High vegetative reproduction through propagules and clonal growth predominates here. In the upper montane zone near timberline, the bryophytes of the Peruvian Andes likewise exhibit **short** and **tall turfs** of other upper montane forests but also **"tails."** They retain the rill-like leaf arrangement seen in the humid montane zone and commonly have a central strand, as seen in bryophytes of other upper montane forests. These bryophytes put forth a high sexual reproductive effort, producing numerous sporophytes on a regular basis, a pattern of change toward timberline also seen in Southeast Asia and Central Africa.



Figure 127. Andes at Huandoy, Peru. Photo by Clarquitecto, through Creative Commons.

It is noteworthy that the development of **anisospory** (in bryophytes refers to a bimodal size difference between spores produced in the same sporangium) and **heterospory** (having spores of two sizes) occurs within the tropical Andean forests (Figure 128) (Kürschner & Parolly 1998a), although it can be argued that bryophytes lack true heterospory (see Volume 1, Chapter 3-3 on Sexuality: Size and Sex Differences). Anisosporous bryophytes in the **perennial shuttle** category exhibit the development of **dwarf males** (males epiphytic on females) with no size differentiation visible among the spores. In other cases, true size differences occur, where small male spores and large female spores occur in the same capsule, for example, in *Macromitrium* spp. (Figure 129) and *Phyllogonium fulgens* (Figure 130). *Leptodontium viticulosoides* (Figure

131) exhibits a functional heterospory in which small spores are able to travel long distances, whereas the larger spores are more adaptive for short distances and a quick start for the protonema upon germination – an ideal shuttle strategy.



Figure 128. Tropical Andean forest. Photo by Samuel Rengifo, through Creative Commons.



Figure 129. *Macromitrium sulcatum*, in a genus with two spore sizes, on *Careya arborea*. Photo by Shyamal L., through Creative Commons.



Figure 130. *Phyllogonium fulgens*, a species that has two spore sizes and genders. Photo by Michael Lüth, with permission.



Figure 131. *Leptodontium viticulosoides*, a species with small and large spores that are not separated by gender. Photo by Claudio Delgadillo Moya, with permission.

Physiological adaptations necessarily include tolerance to desiccation and in some cases resistance to drying. Akande (1985) found that the corticolous liverworts *Frullania spongiosa* (see Figure 72) and *Mastigolejeunea florea* (see Figure 132) had higher osmotic potentials than the mosses *Stereophyllum nitens* (see Figure 133) and *Calymperes palisotii* (Figure 134) in his Nigerian study. This potential increased from wet to dry season, presumably making it easier for them to extract water from dew and fog.



Figure 132. *Mastigolejeunea auriculata*; *M. florea* is a leafy liverwort that uses high osmotic potentials to maintain hydration. Photo by Blanka Aguero, with permission.



Figure 133. *Stereophyllum wightii*; *S. nitens* has a low osmotic potential when compared with *Mastigolejeunea florea*. Photo by Michael Lüth, with permission.



Figure 134. *Calymperes palisotii*, a species with a low osmotic potential when compared with *Mastigolejeunea florea*. Photo by Scott Zona, with permission.

Life Cycle Strategies

Understanding the climate and soil parameters that define the bryophyte distributions is just a beginning of our understanding of the limitations of distribution. The physiology and reproductive biology of the bryophytes are likely to be major factors in their distribution. Maciel-Silva *et al.* (2012) examined reproductive performance as influenced by altitude in both monoicous and dioicous bryophytes in the Brazilian Atlantic rainforest. They sought to separate effects of reproductive strategy from effects of habitat. Using 11 species of bryophytes, they measured reproductive performance of sexual branches, sex organs, fertilization, and sporophyte production at sites from sea level to the montane region during 15 months. As is typical, monoicous bryophytes had the highest reproductive performance, with more sexual branches, fertilized eggs, and capsule production. At sea level, bryophytes produced more sexual branches and had more female-biased sex ratios than did those in the montane site. Nevertheless, the sporophyte frequency was similar between sea level and montane zones. Fertilization occurred mostly during periods of heavy rains (October to December). But habitat is also important in influencing life-history differences. The high production of reproductive structures early in the reproductive phase seems to compensate for the female-biased sex ratios and low fertilization rates. Maciel-Silva and Valio (2011) found similar phenological characteristics in the reproduction of bryophytes from sea level and the montane region of Brazil.

Santos *et al.* compared monoicous vs dioicous species numbers at five altitudes at Serra do Mar State Park, Brazil. The pattern is interesting because the ratio of dioicous to monoicous is highest at sea level, then drops, and again rises at 1200 m. This ratio is even more pronounced for liverworts than for mosses. The monoicous condition increased with altitude except on the mountaintop (1200 m). The researchers suggested that asexual reproduction

may permit species to live in conditions that are unfavorable to fertilization, particularly for dioicous taxa.

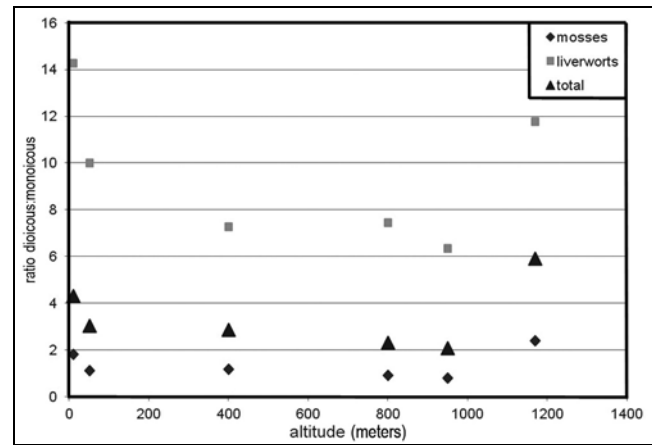


Figure 135. Dioicous-monoicous comparison for bryophytes at five altitudes at Serra do Mar State Park, Brazil. Modified from Santos *et al.* 2017.

Frey *et al.* (1995) examined the life strategies of epiphytic bryophytes on an altitudinal gradient from tropical lowland and montane forest, ericaceous woodlands, and the *Dendrosenecio* (Figure 136-Figure 137) subpáramo of the eastern Congo basin and adjacent mountains as part of the BRYOTROP expedition. They identified three strategies: **colonists**, **perennial shuttle species**, and **perennial stayers**. But only the **perennial stayers** seem to be important, an indication of the more constant ecological conditions and long-lasting microsites for epiphytes. These conclusions were based on both sociological investigations and determination of mean percentage cover values in each of the life strategy categories. In the tropical lowland and lower montane zone forests the **perennial shuttle** species and **perennial stayers** with moderately low or low sexual and asexual reproductive effort are most common. This strategy is suitable for the high temperatures and humidity levels in these zones. In the montane rainforests and cloud forests of the upper montane zone, the **perennial shuttle** species is still dominant, but has high asexual reproductive activity using propagules and clonal growth. In the secondary forests of this zone and in the ericaceous woodlands and subpáramo of African volcanoes (Figure 138), the **perennial shuttle** and **perennial stayers** are dominant, using high levels of sexual reproduction and producing sporophytes regularly here and in the subalpine-alpine zone. Such a strategy is typical for epiphytes under xeric conditions. Thus, life cycle strategy seems to be important as an adaptation to the changing conditions that arise with elevational change.



Figure 136. *Dendrosenecio*, a genus typical of the subpáramo of the eastern Congo basin, Rwenzori Mountains National Park, Africa. Photo by Agripio, through Creative Commons.



Figure 137. *Dendrosenecio*, a genus in the subpáramo of the eastern Congo basin. Photo through Creative Commons.



Figure 138. Páramo on Mt. Cameroon old lava flows. Photo by Amcaja, through Creative Commons.

In the Neotropics, Batista *et al.* (2018) studied life forms in the humid forest of Chapada do Araripe, Ceará State, Brazil. This region experiences seasonal rainfall. The predominant life forms are the desiccation-tolerant **turfs** and intermediate **mat** and **weft** (67%) life forms (Figure 139). Few low-tolerance species (3%) were present. Turfs were further divided into **turf** and **sparse turf**. **Mats** also included **thallose mats**. The monoicous life strategy predominated (67%), with 75 % of those with asexual reproductive means (gemmae, regenerating fragments, and caducous leaves) being dioicous species (Figure 140).

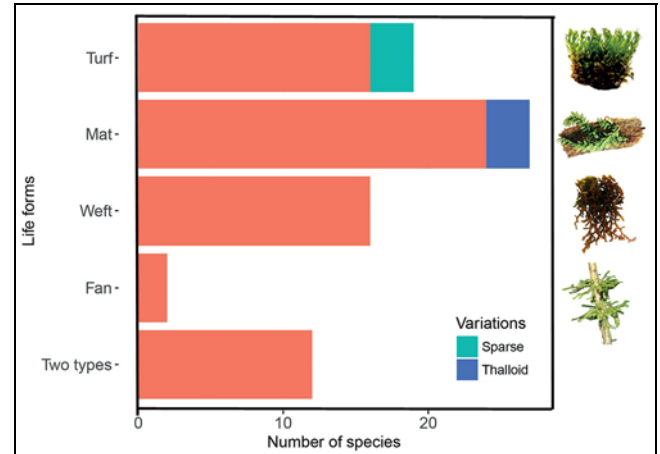


Figure 139. Number of species in the represented life forms in the humid portion of northeastern Brazil. Modified from Batista *et al.* 2018.

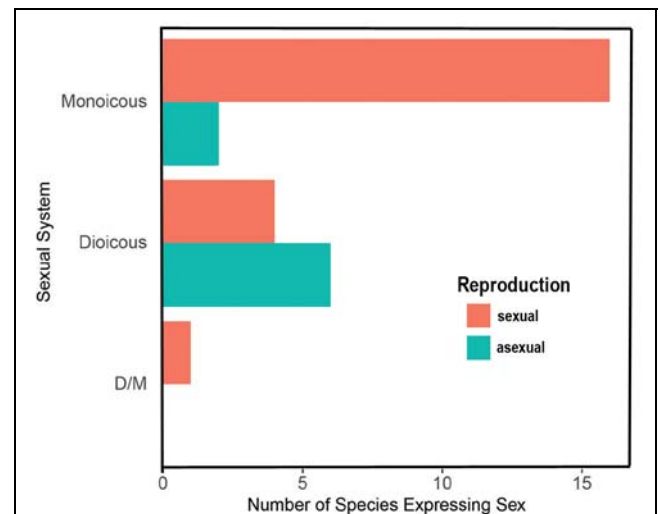


Figure 140. Sexual vs asexual reproductive strategies in the humid portion of northeastern Brazil. Modified from Batista *et al.* 2018.

Batista *et al.* (2018) also examined substrate preferences. Bark epiphytes were by far the most species rich (Figure 141). Some preferred rocks or soil, but the number without any substrate preference was large, exceeded only by bark species.

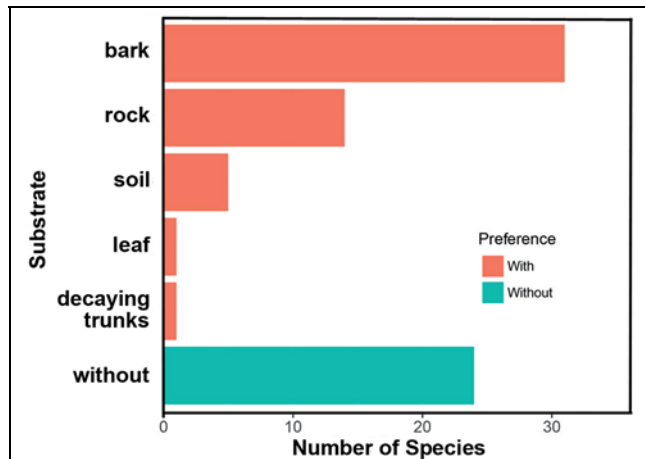


Figure 141. Numbers of species **with** substrate preferences, on tree bark, rocks, soil, leaves, and on decaying tree trunks in the humid portion of northeastern Brazil. Species that colonize more than one type of substrate (two types) and those that do not demonstrate any preference (**without**). Modified from Batista *et al.* 2018.

Silva *et al.* (2014) found that mean diurnal temperature range explained habitat suitability for 9 of the 10 indicator species they used from the Brazilian Atlantic Forest. This can explain the altitudinal distribution of bryophytes.

Summary

High elevations near the equator have similar bryophytes to those at lower elevations farther from the equator. Tropical bryophyte diversity and abundance both increase from lowlands to montane regions. Bryophytes throughout most of the humid tropics have the same altitudinal zonation patterns: lowland forest, submontane forest, upper lower montane forest, montane forest, and subalpine forest, mimicking the zonation patterns of tracheophytes and correlating with temperature and available moisture. Bryophytes, therefore, serve as good indicators of the zones.

In southeastern Brazil, **dioicous** species predominate in all elevations, with the smallest dioicous:monoicous ratio at mid elevations. **Endemism** increases with elevation, but in some locations, endemism can be very low. The highest elevation records of bryophytes are mostly in the tropics. The greatest species richness typically occurs below the alpine zone. The **α diversity** in the Andes is typically similar, but **β diversity** and **γ diversity** in the Andes are much greater.

Species presence and percent cover seem to be of equal importance in distinguishing bryophyte zones. These are highest in the **condensation zones**. Higher elevations tend to have more moisture and greater species richness. At low elevations, light intensity barely exceeds the **light compensation point**, greatly limiting productivity. This problem is exacerbated by the high temperatures, as supported by transplant studies. Mosses do not support **Rapoport's elevational rule** (prediction of trends of increased elevational ranges of plants with increase in elevation). It is likely

that genetic races will emerge as we examine molecular data for the species that occur in multiple zones.

Both abundance and biomass of epiphytic bryophytes increase from the lowlands to the **treeline**. Both low and high water content severely limit photosynthesis. **Perennial stayers** and **perennial shuttle species** predominate throughout the elevations, but life forms change from **mat** forms of the lowlands to **dendroid**, **pendent**, **fan**, and **weft** forms that can extract moisture from fog in higher elevations of the montane. **Cushions** become common in the alpine zone. Sea level bryophytes may produce more sexual branches and have more female-biased sex ratios than do those in the montane zone. The **perennial shuttle** species is still dominant in the montane zone, but has high asexual reproductive activity using propagules and clonal growth.

Acknowledgments

S. Robbert Gradstein was invaluable in providing me with papers, images, and constructive criticism on this subchapter.

Literature Cited

- Ah-Peng, C., Chuah-Petiot, M., Descamps-Julien, B., Bardat, J., Stamenoff, P., and Strasberg, D. 2007. Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Réunion. *Divers. Distrib.* 13: 654-662.
- Ah-Peng, C., Wilding, N., Kluge, J., Descamps-Julien, B., Bardat, J., Chuah-Petiot, M., Strasberg, D., and Hedderson, T. A. 2012. Bryophyte diversity and range size distribution along two altitudinal gradients: continent vs. island. *Acta Oecol.* 42: 58-65.
- Akande, A. O. 1985. Osmotic potential – A factor for resistance to water stress in some Nigerian species of corticolous bryophytes. *Trop. Ecol.* 26: 80-84.
- Ashton, P. S. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspec. Plant Ecol. Evol. Syst.* 6: 87-104.
- Azuelo, A. G., Sariana, L. G., and Pabualan, M. P. 2010. Diversity and ecological Status of bryophytes in Mt. Kitanglad, Bukidnon. *Asian J. Biodiv. Ecol. Div. Sec.* 1(1): 49-71.
- Bader, M. Y., Wagner, S., and Zotz, G. 2013. Current and future carbon balances of bryophytes in the warm tropics. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.
- Batista, W. V. S. M., Pôrto, K. C., and Santos, N. D. 2018. Distribution, ecology, and reproduction of bryophytes in a humid enclave in the semiarid region of northeastern Brazil. *Acta Bot. Brasil.* 32: 303-313.
- Biebl, R. 1964. Temperaturresistenz tropischer Pflanzen auf Puerto Rico. *Protoplasma* 59: 133-156.
- Bryant, E. H., Crandall-Stotler, B., and Stotler, R. E. 1973. A factor analysis of the distribution of some Puerto Rican liverworts. *Can. J. Bot.* 51: 1545-1554.
- Chantanaorrapint, S. 2010. Ecological Studies of Epiphytic Bryophytes along Altitudinal Gradients in Southern Thailand. Ph.D. dissertation, Rheinische Friedrich-Wilhelms-Universität, Bonn. V + 107 pp.

- Churchill, S. P. 1991. The floristic composition and elevational distribution of Colombian mosses. *Bryologist* 94: 157-167.
- Churchill, S. P., Griffin, D. III, and Lewis, M. 1995. Moss diversity of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). *Biodiversity and conservation of Neotropical montane forests*. New York Botanical Garden, Bronx, New York, pp. 335-346.
- Cornelissen, J. H. C. and Gradstein, S. R. 1990. On the occurrence of bryophytes and macrolichens in different lowland rain forest types at Mabura Hill, Guyana. *Trop. Bryol.* 3: 29-35.
- Costa, D. P., Santos, N. D., Rezende, M. A., Buck, W. R., and Schäfer-Verwimp, A. 2015. Bryoflora of the Itatiaia National Park along an elevation gradient: Diversity and conservation. *Biodiv. Conserv.* 24: 2199-2212.
- Delgadillo, C. M. and Cardenas, A. S. 1989. Phytogeography of high-elevation mosses from Chiapas, Mexico. *Bryologist* 92: 461-466.
- Eggers, J. 2001. Epiphyllous Lejeuneaceae in Costa Rica. Contributions to the altitudinal distribution of selected species. *Trop. Bryol.* 20: 109-115.
- Enroth, J. 1990. Altitudinal zonation of bryophytes on the Huon Peninsula, Papua New Guinea. *Trop. Bryol.* 2: 61-90.
- Frahm, J.-P. 1987. Ökologische Studien an der epiphytische Moosvegetation in Regenwäldern NE-Perus. In: *Ergebnisse der BRYOTROP Expedition nach Peru 1982*. Beih. Nova Hedw. 88: 143-158.
- Frahm, J.-P. 1990a. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedw.* 51: 151-164.
- Frahm, J.-P. 1990b. Bryophyte phytomass in tropical ecosystems. *Bot. J. Linnean Soc.* 104: 22-33.
- Frahm, J.-P. 1990c. The altitudinal zonation of bryophytes on Mt. Kinabalu. *Nova Hedw.* 51: 133-149.
- Frahm, J.-P. 1990d. The ecology of epiphytic bryophytes on Mt. Kinabalu, Sabah (Malaysia). *Nova Hedw.* 51: 121-132.
- Frahm, J.-P. 1994a. Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda 1. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire). *Trop. Bryol.* 9: 137-152.
- Frahm, J.-P. 1994b. Scientific Results of the BRYOTROP Expedition to Zaire and Rwanda 2. The altitudinal zonation of the bryophytes on Mt. Kahuzi (Zaire). *Trop. Bryol.* 9: 153-168.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Frahm, J. P., Pócs, T., O'Shea, B., Koponen, T., Piipo, S., Enroth, J., Rao, P.-C., and Fang, Y. 2003. *Manual of Tropical Bryology*. *Trop. Bryol.* 23: 1-200.
- Freiberg, M. and Freiberg, E. 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. *J. Trop. Ecol.* 5: 673-688.
- Frey, W., Kürschner, H., and Seifert, U. H. 1995. Scientific Results of the BRYOTROP expedition to Zaire and Rwanda. 7. Life strategies of epiphytic bryophytes from tropical lowland and montane forests, Ericaceous woodlands and the *Dendrosenecio* subpáramo of the eastern Congo basin and adjacent mountains (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). *Trop. Bryol.* 11: 129-150.
- Frey, G., Frey, W., and Kürschner, H. 2012. High altitude bryophytes from the Cordillera Real in Bolivia. *Nova Hedw.* 95: 165-182.
- Germano, S. R. and Pôrto, K. C. 2006. Bryophyte communities in Atlantic forest remnant, state of Pernambuco, Brazil. *Cryptog. Bryol.* 27: 153-163.
- Glime, J. M., Hudy, P. S., and Hattori, S. 1990. Diversity and altitudinal niche width characteristics for 35 taxa of the Papua New Guinea *Frullania* flora with consideration of sibling pairs. *Trop. Bryol.* 2: 103-117.
- Gradstein, S. R. 1995. Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). *Biodiversity and conservation of Neotropical montane forests*. New York Botanical Garden, Bronx, New York, pp. 321-334.
- Gradstein, S. R. and Frahm, J.-P. 1987. Die floristische Höhengliederung der Moose entlang des BRYOTROP-Transektes in NOPeru. [The floristic elevation of the mosses along the BRYOTROP transect in NOPeru.]. *Beih. Nova Hedw.* 88: 105-113.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies*. Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R. and Salazar Allen, N. 1992. Bryophyte diversity along an altitudinal gradient in Darién National Park, Panama. *Trop. Bryol.* 5: 61-72.
- Gradstein, S. R. and Sipman, H. J. M. 1978. Taxonomy and world distribution of *Campylopus introflexus* and *C. pilifer* (= *C. polytrichoides*): A new synthesis. *Bryologist* 81: 114-121.
- Gradstein, S. R. and Vána, J. 1987. On the occurrence of Laurasian liverworts in the tropics. *Mem. N. Y. Bot. Gard.* 45: 388-425.
- Gradstein, S. R., Pócs, T., and Vána, J. 1983. Disjunct Hepaticae in tropical America and Africa. *Acta Bot. Hung.* 29: 127-171.
- Gradstein, S. R., Reenen, G. B. A. van, and Griffin, D. III. 1989. Species richness and origin of the bryophyte flora of the Colombian Andes. *Acta Bot. Neerl.* 38: 439-448.
- Gradstein, S. R., Montfoort, D., and Cornelissen, J. H. C. 1990. Species richness and phytogeography of the bryophyte flora of the Guianas, with special reference to the lowland forest. *Trop. Bryol.* 2: 117-126.
- Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001a. *Guide to the Bryophytes of Tropical America*. *Mem. N. Y. Bot. Gard.* 86: 1-577.
- Gradstein, S. R., Griffin, D. III, Morales, M. I., and Nadkarni, N. M. 2001b. Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia* 23: 203-212.
- Grau, O., Grytnes, J. A., and Birks, H. J. B. 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *J. Biogeogr.* 34: 1907-1915.
- Grieve, I. C., Proctor, J., and Cousins, S. A. 1990. Soil variation with altitude on volcan Barva, Costa Rica. *Catena* 17: 525-534.
- Grolle, R. 1966. Die Lebermoose Nepals. *Ergeb. Forsch.-Unternehm. Nepal Himalaya* 1(4): 262-298.
- Grubb, P. J. 1974. Factors controlling the distribution of forest-types on tropical mountains: New facts and a new perspective. In: Flenley, J. R. (ed.). *Altitudinal zonation in Malesia*. Univ. of Hull. Misc. Series 16: 13-45.
- Grubb, P. J. and Whitmore, T. C. 1966. A comparison of montane and lowland rain forest in Ecuador: II. The climate and its effects on the distribution and physiognomy of the forests. *J. Ecol.* 54: 303-333.
- Hedberg, O. 1951. Vegetation belts of the East African mountains. *Svensk Bot. Tidskr.* 45: 140-202.

- Hemp, A. 2002. Ecology of the pteridophytes on the southern slopes of Mt. Kilimanjaro – I. Altitudinal distribution. *Plant Ecol.* 159: 211-239.
- Kessler, M. 2000. Altitudinal zonation of Andean cryptogam communities. *J. Biogeogr.* 27: 275-282.
- Kitayama, K. and Mueller-Dombois, D. 1992. Vegetation of the wet windward slope of Haleakala, Maui, Hawaii. *Pacific Sci.* 46: 197-220.
- Kluge, J., Kessler, M., and Dunn, R. R. 2006. What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecol. Biogeogr.* 15: 358-371.
- Konrat, M. von. 2017. Are epiphytic bryophyte communities characterized by changes along an elevational gradient? A preliminary study on eastern Viti Levu, Fiji Islands. *Bryo. Div. Evol.* 39: 28-37.
- Kürschner, H. 1995. Wissenschaftliche Ergebnisse der BRYOTROP-Expedition nach Zaire und Rwanda. 5. Höhengliederung epiphytischer Moose im östlichen Kongobecken und den angrenzenden Gebirgsstöcken (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe/Rwanda). [Scientific results of the BRYOTROP expedition to Zaire and Rwanda. 5. Elevation of epiphytic mosses in the eastern Congo basin and the adjacent mountain ranges (Parc National de Kahuzi-Biega/Zaire, Forêt de Nyungwe / Rwanda).]. *Trop. Bryol.* 11: 77-86.
- Kürschner, H. and Parolly, G. 1998a. Lebensstrategien stammepiphytischer Moose in regenwaldern am andenostabhang und im Amazonas-Tiefland von nord-Peru. [Life strategies of epiphytic bryophyte vegetation in rainforests along the eastern Andean slopes and the Amazon lowlands of northern Peru]. *Nova Hedw.* 67: 1-22.
- Kürschner, H. and Parolly, G. 1998b. Lebensformen und adaptationen zur wasserleitung und wasserspeicherung in epiphytischen moosgesellschaften nord-Perus (Amazonas-tiefland, cordillera oriental, cordillera central). [Life forms and adaptations to water conduction and water storing in epiphytic bryophyte communities in northern Peru (the Amazon lowlands, eastern and central cordillera).]. *Nova Hedw.* 67: 349-379.
- Kürschner, H., Frey, W., and Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – A pantropical synopsis. *Nova Hedw.* 69: 73-99.
- Lewis, B. A., Phillipson, P. B., Andrianarisata, M., Rahajasoja, G., Rakotomalaza, P. J., Randriambololona, M., and McDonagh, J. 1996. A study of the botanical structure, composition, and diversity of the eastern slopes of the Reserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation, Sept 1996. *Fieldiana* 85: 24-71.
- Li, Y., Glime, J. M., and Liao, C. 1992. Responses of two interacting *Sphagnum* species to water level. *J. Bryol.* 17: 59-70.
- Maciel-Silva, A. S. and Valio, I. F. M. 2011. Reproductive phenology of bryophytes in tropical rain forests: The sexes never sleep. *Bryologist* 114: 708-719.
- Maciel-Silva, A. S., Valio, I. F. M., and Rydin, H. 2012. Altitude affects the reproductive performance in monoicous and dioicous bryophytes: Examples from a Brazilian Atlantic rainforest. *AoB Plants* 2012, pls016.
- Nekesa, W. S. 2015. The distribution of two major plant groups (bryophytes and tracheophytes) along an altitudinal gradient on Naro Moru Track, Mount Kenya. M.S. thesis, University of Nairobi.
- Nöske, N. M., Gradstein, S. R., Kürschner, H., Parolly, G., and Torracchi, S. 2003. Cryptogams of the Reserva Biológica San Francisco (Province Zamora-Chinchipe, southern Ecuador) I. Bryophytes. *Cryptog. Bryol.* 24: 15-32.
- Ohsawa, M. 1995. The montane cloud forest and its gradational changes in Southeast Asia. In: Lawrence S. Hamilton, L. S., Juvik, J. O., and Scatena, F. N. *Tropical Montane Cloud Forests.* *Ecol. Stud.* 110: 254-265.
- Oyesiku, O. O. 2013. Bryophyte diversity and altitudinal distribution in tropical rainforest of southwest Nigeria. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.
- Pócs, T. 1976. Bioclimatic studies in the Uluguru Mountains (Tanzania. East Africa), II. Correlations between orography, climate and vegetation. *Acta Bot. Acad. Sci. Hung.* 22: 163-183.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology.* Chapman and Hall, London, pp. 59-104.
- Pócs, T. 1984. The altitudinal distribution of Kilimanjaro bryophytes. In: Seyani, J. H. and Chikuni, A. C. *Proc. XIIIth Plenary Meeting AETFAT, Malawi* 2: 797-812.
- Pôrto, K. C. 1992. Bryoflores d'une forêt de plaine et d'une forêt d'altitude moyenne dans l'état de Pernambuco (Brasil). 2. Analyse écologique comparative des forêts. [Bryoflora of a lowland forest and submontane forest in Pernambuco state, Brazil. 2. Comparative ecological analysis of the forests.]. *Cryptog. Bryol. Lichenol.* 13: 187-219.
- Potemkin, A. D., Doroshina, G. Y., and Mikhalenko, V. N. 2018. Liverworts and mosses at the top of Elbrus (Caucasus) and bryophytes near limits of their altitudinal distribution. *Novosti Sist. Nizsh. Rast.* 52(1): 183-193.
- Reenen, G. B. A. van. 1987. Altitudinal bryophyte zonation in the Andes of Colombia: A preliminary report. *Symp. Biol. Hung.* 35: 631-637.
- Reenen, G. B. A. van and Gradstein, S. R. 1983. Studies on Colombian cryptogams. XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Bot. Neerl.* 32: 163-175.
- Reenen, G. B. A. van and Gradstein, S. R. 1984. An investigation of bryophyte distribution and ecology along an altitudinal gradient in the Andes of Colombia. *J. Hattori Bot. Lab.* 56: 79-84.
- Richards, P. W. 1984a. The ecology of tropical forest bryophytes. In: Schuster, R. M. (ed.). *New Manual of Bryology.* Vol. 2. Hattori Botanical Laboratory, Nichinan. pp. 1233-1270.
- Richards, P. W. 1984b. Introduction. In Dyer, A. F. and Duckett, J. G. (eds.). *The Experimental Biology of Bryophytes*, Academic Press, New York, pp. 1-8.
- Rodriguez, R. 2015. Symbiosis on Mt. Everest. Adventurers and Scientists for Conservation (ASC). Power Point Poster. USGS.
- Rydin, H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos* 45: 374-379.
- Santos, N. D. and Costa, D. P. 2010. Altitudinal zonation of liverworts in the Atlantic Forest, Southeastern Brazil. *Bryologist* 113: 631-645.
- Santos, N. D., Costa, D. P., Kinoshita, L. S., and Shepherd, G. J. 2014. Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? *Ecol. Indic.* 36: 431-440.

- Santos, N. D., Costa, D. P., Kinoshita, L. S., and Shepherd, G. J. 2017. Variations in bryophyte communities in a short elevational gradient in Atlantic Forest of southeastern Brazil. *Cryptog. Bryol.* 38: 191-211.
- Schiavone, M. M. and Suárez, G. M. 2009. *Globulinella halloyi* (Pottiaceae), a new species from Argentina. *Bryologist* 112: 584-588.
- Seifriz, W. 1924. The altitudinal distribution of lichens and mosses on Mt. Gede, Java. *J. Ecol.* 12: 307-313.
- Silva, M. P., Kamino, L. H., and Pôrto, K. C. 2014. Is the current network system of protected areas in the Atlantic Forest effective in conserving key species of bryophytes? *Trop. Conserv. Sci.* 7: 61-85.
- Song, L., Ma, W.-Z., Yao, Y.-L., Liu, W.-Y., Li, S., Chen, K., Lu, H.-Z., Cao, M., Sun, Z.-H., Tan, Z.-H., and Nakamura, A. 2015. Bole bryophyte diversity and distribution patterns along three altitudinal gradients in Yunnan, China. *J. Veg. Sci.* 26: 576-587.
- Stadtmüller, T. 1987. Cloud forests in the humid tropics. United Nations University, Costa Rica, 81 pp.
- Stam, Å, Enroth, J., Malombe, I., Pellikka, P., and Rikkinen, J. 2017. Experimental transplants reveal strong environmental effects on the growth of non-vascular epiphytes in Afrotropical forests. *Biotropica* 49: 862-870.
- Stech, M. and Wagner, D. 2005. Molecular relationships, biogeography, and evolution of Gondwanan *Campylopus* species (Dicranaceae, Bryopsida). *Taxon* 54: 377-382.
- Sun, S. Q., Wu, Y. H., Wang, G. X., Zhou, J., Yu, D., Bing, H. J., and Luo, J. 2013. Bryophyte species richness and composition along an altitudinal gradient in Gongga Mountain, China. *PLoS ONE* 8: 1-10.
- Troll, C. 1948. Der asymmetrische Aufbau der Vegetationszonen und Vegetationsstufen auf der Nord- und Südhalbkugel. *Jahresbericht der Geobotanisches Forschungsinstitutes Rubel i Zurich f. 1947, Zurich*, pp. 46-83.
- Tusiime, F. M., Byarujali, S. M., and Bates, J. W. 2007. Diversity and distribution of bryophytes in three forest types of Bwindi Impenetrable National Park, Uganda. *Afr. J. Ecol.* 45: 79-87.
- Wagner, S., Zotz, G., Salazar Allen, N., and Bader, M. Y. 2012. Altitudinal changes in temperature responses of net photosynthesis and dark respiration in tropical bryophytes. *Ann. Bot.* 111: 455-465.
- Wang, J., Vanderpoorten, A., Hagborg, A., Goffinet, B., Laenen, B., and Patino, J. 2016. Evidence for a latitudinal diversity gradient in liverworts and hornworts. *J. Biogeogr.* 2016: 1-2.
- Wolf, J. H. D. 1989. Comunidades epífitas en un transecto altitudinal en la Cordillera Central, Colombia: Datos iniciales sobre la cantidad de especies de briófitas y líquenes. [Epiphytic communities in an altitudinal transect in the Cordillera Central, Colombia: Initial data on the amount of bryophytes and lichens.]. In: Hammen, T. van der, Diaz-Piedrahita, S., and Alvarez, V. J. (eds.). *Studies on Tropical Andean Ecosystems*, 3. J. Cramer, Vaduz, pp. 455-459.
- Wolf, J. D. H. 1992. Species richness patterns of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Selbyana* 13: 166-167.
- Wolf, J. H. D. 1993a. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the northern Andes. *Ann. Missouri Bot. Gard.* 80: 928-960.
- Wolf, J. H. D. 1993b. Ecology of epiphytes and epiphytes communities in montane rain forests, Colombia. Ph.D. dissertation, University of Amsterdam, The Netherlands.
- Zhang, D.-C., Li, X.-J., and Si, He. 2007. Bryaceae. Moss Flora of China. English version. Vol. 4. St. Louis, pp. 3-92.
- Zhang, Li. 2001. Diversity and conservation of Hong Kong bryophytes. Ph.D. thesis, The University of Hong Kong, ix + 303 pp.
- Zotz, G. 1999. Altitudinal changes in diversity and abundance of non-vascular epiphytes in the tropics – an ecological and ecophysiological explanation. *Selbyana* 20: 257-260.
- Zotz, G., Büdel, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO₂ exchange of tropical bryophytes in a lower montane rainforest in Panama. *Bot. Acta* 110: 9-17.

CHAPTER 8-9

TROPICS: SUBMONTANE AND MONTANE

TABLE OF CONTENTS

Submontane.....	8-9-2
Montane Forests	8-9-5
Lower Montane.....	8-9-13
Upper Montane	8-9-18
Summary	8-9-30
Acknowledgments.....	8-9-30
Literature Cited	8-9-30

CHAPTER 8-9

TROPICS: SUBMONTANE AND MONTANE



Figure 1. Ecuadorian mountains and cloud forest. Photo by Arthur Anker, with permission.

Altitudinal zonation of bryophytes in the humid tropics are similar throughout the world (Frahm & Gradstein 1991). This subchapter will discuss zonation of the submontane and montane zones.

Submontane

The submontane region in Dominica are influenced primarily by the presence or absence of the canopy tree *Amanoa caribaea* (DeWalt *et al.* 2016). But in addition to that, hurricane disturbance is a major factor.

Aceby *et al.* (2003) compared bryophyte species richness in the submontane rainforest and fallows of Bolivia. The fallows exhibited a significantly decreased diversity of moss species, but the liverwort diversity showed little reduction in species except in the very young fallows. **Smooth mats** were significantly greater in presence in the fallows (72%), probably due to the warmer, drier climate there. Generalists and sun species were the more common members of the fallow communities, with about half of the submontane species occurring there. The specialists are slower to become re-established. The submontane exhibits the highest species richness in the

canopy, whereas the fallows reaches its highest diversity in the understory. This was in part due to the shifting of typical **rough mats**, **fans**, and **tails** to the lower heights in the fallows where the air temperature and humidity were more similar to those of the montane forest.

In central Sulawesi (Figure 2), Sporn *et al.* (2010) found 146 epiphytic species. They noted that this was among the highest number of epiphytic bryophyte species reported for any tropical forests, suggesting that the Malesian region is a global biodiversity hotspot. Among these bryophytes, 45% of the species were restricted to the tree crowns. The **dendroid** and **fan**-like species were in the understory; **tufts** dominated in the tree crowns.

Valdevino *et al.* (2002) reported on the pleurocarpous mosses (*e.g.* Figure 21-Figure 22) from a submontane rainforest in Pernambuco State, Brazil. They found only 23 pleurocarpous moss species in the 700 ha of their study of valleys and hills at 900-1,120 m asl.

Sonnleitner *et al.* (2009) found that even the smallest disturbance of the forest canopy could alter the microclimate and have a negative impact on the epiphyll community in the tropical lowland rainforest in Costa Rica (Figure 3).



Figure 2. Rice field with coffee and cacao plantations and submontane rainforest in the background, Sulawesi. Photo courtesy of S. Robbert Gradstein.



Figure 3. Submontane rainforest Costa Rica. Photo courtesy of S. Robbert Gradstein.

The strong response of epiphyllous (Figure 4) bryophytes to even subtle microclimatic variations suggests that undisturbed forest canopies and their control on microclimate may be essential for the development of epiphyll communities.



Figure 4. Epiphylls on a leaf. Photo by Rafael Medina, with online permission.

In a submontane tropical rainforest in Panama (Figure 5), Zotz *et al.* (1997) found that water relations were important. Both low and high water contents reduced carbon gain. Low light levels such as those found during a rainstorm were less important. They found a net carbon gain for the year for the mosses and liverworts to be 45%.



Figure 5. Panamanian sub-montane and montane rainforests. Photo by S. B. Matherson, through Creative Commons.

One of the factors that can affect productivity is nitrogen availability. Bryophytes can't use atmospheric nitrogen, but nitrogen fixation by associated organisms contributes to their nitrogen supply. Matzek and Vitousek (2003) found that when leaves had low N:P ratios, the N fixation was greater.

In the Colombian Andes (Figure 6), Gradstein *et al.* (1989) found that liverworts outnumber the mosses in both upper submontane and montane forests on the western slopes, but in drier environments their species numbers are lower than those of mosses. Species richness increases with altitude to the upper montane forest. Furthermore, at the lower altitudes, the wide-ranging tropical species are most prevalent.



Figure 6. Ritacuba Blanco, in the Andes of Colombia. Photo by 2005biggar, through Creative Commons.

Kürschner *et al.* (1999) described, for the first time, the pantropical patterns of life forms, life strategies, and ecomorphological structures of bryophytes inhabiting tree trunks. These represented altitudinal variations in transects in Southeast Asia, Africa, and South America. They considered the **mat-forming perennial stayers** and **perennial shuttle** species to characterize the tropical lowlands and submontane belt. In Ecuador, Kürschner and Parolly (2005) compared life forms in submontane and montane epiphytic bryophyte communities. The life forms are actually functional types and can provide considerable information (humidity, water supply, desiccation risk, light climate) about an ecosystem without necessitating species identification. In the submontane region, **mat-forming perennial stayers** and **perennial shuttle species** are the dominant forms, forming the *Symbiezidium transversalis* (Figure 7)-*Ceratolejeunea cubensis* (Figure 8) alliance. These are replaced by **fan** and **weft** life forms of **perennial stayers** and **perennial shuttle species** in the more montane regions, where they can take advantage of the cooler, more humid climate.



Figure 7. *Symbiezidium* sp.; *S. transversalis* is a species indicative of the submontane zone. Photo by Hermann Schachner, through Creative Commons.

Parolly and Kürschner (2004) found that bryophytes in the submontane and montane regions of southern Ecuador fall into two zonal groups. The submontane *Symbiezidium transversalis* (Figure 7)-*Ceratolejeunea cubensis* (Figure 8) has two communities, whereas the montane *Omphalantho filiformis* (*Cheilolejeunea filiformis*; see

Figure 9)-*Plagiochilion apicedentis* (*Plagiochila longiramea*; see Figure 10) has six. There is a slight deviation from the species in these associations in Peru (Figure 11). The epiphytic bryophyte communities correspond "perfectly to the supporting forest types" and thus are useful in defining the vegetation zones.



Figure 8. *Ceratolejeunea cubensis*, a species indicative of the submontane zone. Photo by Scott Zona, with permission.



Figure 9. *Cheilolejeunea* (Lejeuneaceae) from the Neotropics; *Cheilolejeunea filiformis* forms an association with *Plagiochila longiramea* in the Neotropical montane zone. Photo by Michael Lüth, with permission.



Figure 10. *Plagiochila adianthoides* from the Neotropics; *Plagiochila longiramea* forms an association with *Cheilolejeunea filiformis* in the Neotropical montane zone. Photo by Michael Lüth, with permission.



Figure 11. Submontane rainforest in the Peruvian Andes. Photo courtesy of S. Robbert Gradstein.

Montane Forests

Even countries like Ethiopia (Figure 12) and Kenya (Figure 13) that we picture as dry can have distinctive montane bryophyte communities (Hylander *et al.* 2010). In their first collecting trip to the southwestern Ethiopian montane forests (Figure 12), Hylander and coworkers recorded 89 species of liverworts, with 51 of these species new for Ethiopia.



Figure 12. Haremma Forest and Bale Mountains, southeastern Ethiopia. Photo by Sabine's Sunbird, through Creative Commons.



Figure 13. Montane rainforest around Mt Kenya. Photo by Chris 73, through Creative Commons.

These forests not only have a higher altitude, but also have rocky soil types (Pires & Prance 1985). The rocky substrate can create extreme drought, particularly during the short dry periods. At higher elevations there is greater humidity. The air can be saturated, providing a constant mist that is available to the bryophytes. Mosses, lichens, and small ferns form carpets over the rocks, tree trunks, and branches. Where the slopes are not steep, the forest is dense. Trees become smaller with altitude, with the treeline at Serra Neblina, Brazil (Figure 14), at about 2,600 m asl. The flowering plant family Theaceae (Figure 15) becomes prominent at higher altitudes and insectivorous Sarraceniaceae (*Heliamphora*; Figure 16) occur here. Fire is more likely here, but in Guayana the humidity is high and fires are uncommon.



Figure 14. Serra Neblina, where the **Theaceae** is common. Photo by Michellblind, through Creative Commons.



Figure 15. *Gordonia fruticosa* (Theaceae) with bryophytes on the bark. **Theaceae** becomes prominent at higher altitudes at Serra Neblina, Brazil. Photo by David J. Stang, through Creative Commons.



Figure 16. *Heliamphora chimantensis*, an insectivorous plant in the Serra Neblina in Peru. Photo by Andreas Eils, through Creative Commons.

In the Neotropics, the upper montane rainforest (Figure 17) can be distinguished from the lower montane rainforest by the greater percentage of temperate vegetation in the upper one (Churchill *et al.* 1995). The lower montane cloud forests, typically between 1,000 and 2,000 m asl, are characterized by a high percentage of epiphytes and tropical taxa.



Figure 17. Upper montane forest, Pui-Pui, Junín, Peru. Photo by E. Lehr and R. von May, through Creative Commons.

Montane forests have a simpler structure than the lowland forest with a much more luxuriant epiphytic vegetation (Gradstein 1992). The forest floor is often covered with dense carpets of bryophytes, in contrast to the lowland forests. Low temperatures and higher light levels than in the lowland forests support a luxuriant growth of bryophytes up to 15-20 cm thick. These growths may be **tall turfs**, **feather** types, and **pendent** life forms.

The montane forest ecosystems are the most diverse of the highland habitats. In Bolivia, 88% of the liverworts and 74% of the mosses known in the country occur in the montane forest, yet this forest type occupies only 8% of the land (Churchill *et al.* 2009).

Within the highlands the 226 montane forest ecosystems are the most diverse. In Bolivia, for example, montane forests (Yungas and Tucuman-Bolivian) occupy only 8% of the land surface of the country, but contains 88% of the liverworts and 74% of the mosses recorded from the country (Churchill *et al.* 2009).

In the Ecuadorian montane (Figure 18) and lowland rainforest (Figure 19), Grubb *et al.* (1963) found an "exceedingly high" diversity of mosses (2,058 species), suggesting that the tropical Andes might be the richest in species of any tropical region of the world. The tropical Andes have approximately eight times as many species as the Amazon basin. The moss flora supports the vegetation zonation concept, with strong differences between the montane-páramo/puna ground species and the montane forest where epiphytes predominate.

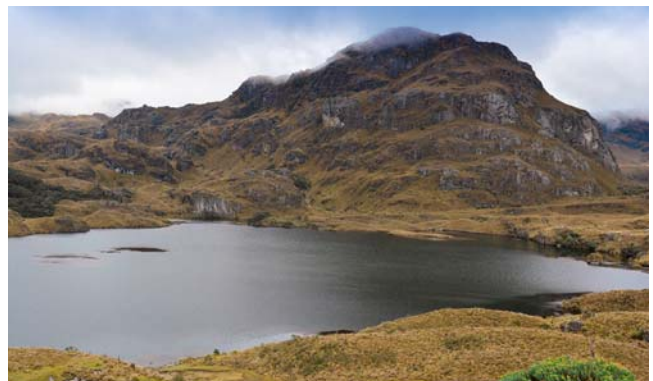


Figure 18. Montane region, El Cajas National Park, Ecuador. Photo by Kate, through Creative Commons.



Figure 19. Ecuador tropical rainforest in middle of Rio Tiguiono at Bataburo Lodge. Photo by Andreas & Christel Noellert, with permission.

In the montane rainforest of Peru, at 2,400 m asl in the Peruvian Yungas, a single tree of *Weinmannia* (Figure 20) sp. was substrate for 110 bryophyte species – 77 liverworts, 32 mosses, and 1 hornwort, a remarkably high species richness (Romanski *et al.* 2011). Using the Johansson zones (lower trunk, upper trunk, mid-crown, mid-outer crown, and outer crown), the researchers found that the upper trunk and large branches of the mid-crown had the highest species richness and abundance. Liverworts, especially *Lejeuneaceae* (Figure 9), dominated all five Johansson zones. (See Gradstein 1995 for additional discussion of the liverwort diversity in the montane forests of the tropical Andes.) The mid-crown enjoys a higher light intensity than the darkness surrounding the lower trunk, coupled with a high relative humidity. Romanski *et al.* distinguished four communities: outer crown, mid to mid-outer crown, upper trunk, and lower trunk. The outer crown had a remarkable 35 liverwort species, joined by only 2 moss species. Of these, 17 of the liverworts had a high light tolerance. This suggests that overall these liverworts have a higher tolerance to high light and exposure.

Costa and Lima (2005) supported previous studies by finding that the moss flora is not uniform in the tropical rainforests of Rio de Janeiro, southeastern Brazil. The lowland, montane, submontane, and upper montane Atlantic rainforests have very different moss floras. The highest number of exclusive species and greatest species richness occur in the montane Atlantic rainforest. The intermediate level of species richness is in the sub-montane Atlantic rainforest. The lowland Atlantic rainforest has the smallest number of species. The high diversity seen in the montane forest is most likely a consequence of the diversity of climatic, edaphic, and physiographic changes present in the macrophytic vegetation. The moss family *Sematophyllaceae* (Figure 21) comprises 19% of the taxa in the lowland forest, the pendent mosses of *Meteoriaceae* (Figure 22) 10% of the montane forests, and *Dicranaceae* (Figure 26) 18% of the upper montane forests. Those taxa having broad Neotropical distributions are important in all these forests. These comprise 40% of the bryophyte taxa. Grubb (1977) contributed additional information on the mineral nutrition in wet tropical mountains.



Figure 20. *Weinmannia trichosperma* trunk with epiphytes. Photo by Lin Liniao, through Creative Commons.



Figure 21. *Sematophyllum* sp. from the Neotropics; *Sematophyllaceae* comprise 19% of the lowland forest bryophyte taxa. Photo by Michael Lüth, with permission.



Figure 22. *Meteorium nigrescens* (Meteoriaceae) from the Neotropics. Photo by Michael Lüth, with permission.

Gradstein and Vána (1994) noted the similarity of the bryophyte community of tropical montane forests of Mexico to that of the boreal community. For example, in the central highlands of the Chiapas, the *Nowellia curvifolia* (Figure 23) community is common on rotten logs and is rich in boreal liverworts. Among these, *Cephalozia catenulata* (Figure 24), *Nowellia curvifolia*, *Campylopodia stenocarpa* (Figure 25), and *Dicranum frigidum* (Figure 26) were the most abundant. The humid flanks of logs typically had *Syzygiella autumnalis* (Figure 27), *Leptoscyphus amphibolius* (see Figure 28), and *Lophozia longiflora* (Figure 29), with *Anastrophyllum hellerianum* (Figure 30-Figure 31) also being frequent. In addition to these locations on logs, *Nowellia curvifolia* is very abundant on logs that have already lost their bark (decorticated logs).



Figure 23. *Nowellia curvifolia*, a common species on rotten logs in the Chiapas. Photo by Štěpán Koval, with permission.



Figure 24. *Cephalozia catenulata*, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.



Figure 25. *Campylopodia ditrichoides* with capsules; *C. stenocarpa* is a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.



Figure 26. *Dicranum frigidum*, a common species on rotten logs in the Chiapas. Photo by Jan-Peter Frahm, with permission.



Figure 27. *Syzygiella autumnalis*, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.



Figure 28. *Leptoscyphus azoricus*; *L. amphibolius* is a common species on rotten logs in the Chiapas. Photo by Jan-Peter Frahm, with permission.



Figure 29. *Lophozia longiflora*, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.



Figure 30. *Anastrophyllum hellerianum* on log. Photo by Michael Lüth, with permission.



Figure 31. *Anastrophyllum hellerianum*, a common species on rotten logs in the Chiapas. Photo by Michael Lüth, with permission.

Among the early south American bryophyte studies was that of Linares (1986). This researcher studied the taxonomic and ecological aspects of the high Andean strip of the El Tabalzo, Cundinamarca, Colombia.

As already noted for epiphytes in earlier subchapters, Veneklaas (1990) reported that the bryophytic epiphytes in the montane rainforests can play a major role in the nutrient dynamics of the rainforest. Veneklaas found that in two epiphyte-rich Andean rainforests of the Central Cordillera of Colombia, the elevation of 2,550 m exhibited a higher nutrient input to the forest through bulk precipitation, at least in part because this elevation has higher total precipitation. At the same time, losses of nutrients from the canopy were also higher, both in total amounts and per unit of precipitation. Bryophytes are able to capture and hold nutrients, often releasing pulses in the first rainfall after a drying period.

Concerned with the role of bryophytes in maintaining water balance and contributing to nutrient cycling in tropical montane forests, Benítez *et al.* (2015) assessed bryophytes and lichens on tree bases of 240 trees in both primary and secondary forests in southern Ecuador (Figure 19). As expected, diversity was higher in primary forests than in monospecific secondary forests. The reduction of canopy diminished bryophyte species. Shade epiphytes were intolerant of the increased light penetration and were replaced by sun epiphytes in the secondary forests.

Bisang *et al.* (2003) explored the diaspore banks in three Malaysian mountain rainforests (Figure 32). They

incubated soil samples from 0-5 cm depth for 15 hours of light daily and mean daily temperature of 19°C with radiation of $3\text{--}5 \mu\text{E m}^{-2} \text{s}^{-1}$. These were kept moist with sterilized water as needed. After 5 months the cultures were gently disturbed with forceps. After 4 and 5 months they were placed under a bright light intensity of $100 \mu\text{E m}^{-2} \text{s}^{-1}$. Liverwort emergence exceeded that of mosses, especially from soils from lower altitudes. Consistent with living bryophytes, the species diversity was twice as high in samples from higher elevations compared to those from lower ones.



Figure 32. Montane rainforest in tropics on Gunung Batu Brinchang, Malaysia. Photo by Peter Coxhead, through Creative Commons.

In Costa Rica, Dauphin L. and Grayum (2005) collected from dry lowland forests and moist montane forests in Guanacaste Province, Costa Rica (Figure 33). In the moist montane forests, **corticolous** (growing on bark) bryophytes predominate. This is in contrast to the soil, log, and rock substrates that are most important in the lowland dry forests. The submontane zone had significantly less species richness. The researchers considered higher temperatures, limiting water availability, and human disturbance as factors limiting the diversity of the submontane zone. Rare species occurred on the tree boles, with 99% of the locally rare species occurring on the tree boles.

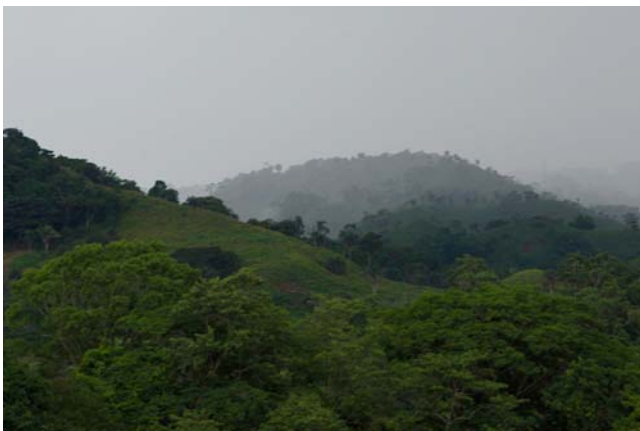


Figure 33. Guanacaste, Costa Rica, montane forests. Photo by Jason Folt, with permission.

Song *et al.* (2015) compared bole bryophytes in three protected forests, one in sub-montane, one in montane, and one in subalpine regions in Yunnan, China (Figure 34). Five plots were established at each of 12 altitudes, using 200 m intervals, totalling 594 subplots. The total number of species identified was 226. Life forms differed among the forest types, with **smooth mat** dominating the sub-montane, **fan** in the montane, and **turf** in the subalpine.



Figure 34. Lowland forest, Guangnan, Yunnan, China. Photo by Anders Johnson, through Creative Commons.

The Itatiaia National Park in Brazil (Figure 35) has well-defined climatic bands of montane, upper montane, and high-altitude fields. Costa *et al.* (2015) used literature, herbarium material, and data banks in addition to examining 10 representative elevations. These sources revealed 519 taxa. As in many other studies, the mid-altitudinal range (2,100-2,200 m asl) had the highest species richness. The number of threatened species increased with elevation. Furthermore, the upper montane forest had the most endemic species (47).



Figure 35. Mountains in Itatiaia National Park, Brazil. Photo by Pedroivan, through Creative Commons.

In Indonesia (Figure 36), submontane forests are known to have a very rich bryophyte flora (Gradstein & Culmsee 2010). On only eight canopy trees, 150 species were present. The researchers found that the lower

montane and upper montane forests of Sulawesi have very different bryophytes that characterize them. The low elevations have mostly mosses in **Calymperaceae** (Figure 37), **Fissidentaceae** (Figure 38), **Hypopterygiaceae** (Figure 93), **Leucobryaceae** (Figure 39), **Meteoriaceae** (Figure 40), **Neckeraceae** (Figure 41), **Pterobryaceae** (Figure 42), and **Thuidiaceae** (Figure 43), and liverworts in **Lejeuneaceae** (Figure 8-Figure 9), **Lophocoleaceae** (Figure 100), **Porellaceae** (Figure 60), **Radulaceae** (Figure 56). By contrast, the high elevations are characterized by the leafy liverworts **Herbertaceae** (Figure 44), **Lepidoziaceae** (Figure 97-Figure 99), **Mastigophoraceae** (Figure 45), **Scapaniaceae** (Figure 46), **Schistochilaceae** (Figure 47), and **Trichocoleaceae** (Figure 102). As is typical, the liverwort family **Lejeuneaceae** has the most species in the submontane and lower montane forests, whereas the leafy liverwort family **Lepidoziaceae** has the most in the upper montane forest. Moss dominance decreases while liverwort dominance increases with elevation. Some of these species prefer rough bark, but none shows a preference for smooth bark. Trunk diameter is important for some species, but communities don't seem to be affected by it.

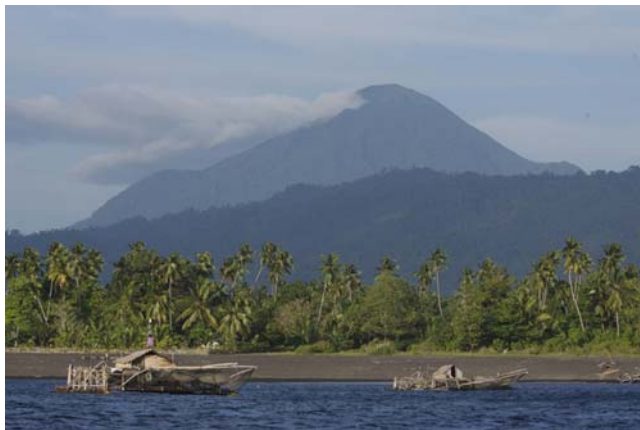


Figure 36. Tangkoko National Park, North Sulawesi, Indonesia, showing mountains in the background. Photo by Lip Kee Yap, through Creative Commons.

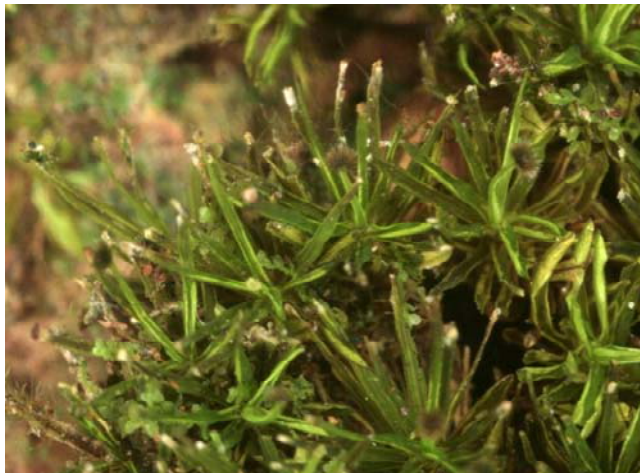


Figure 37. *Calymperes afzelii*, one of the representatives of **Calymperaceae** in Indonesia. Photo by Jan-Peter Frahm, with permission.



Figure 38. *Fissidens nobilis*; *Fissidens* species are common at low elevations in Indonesia. Photo by Janice Glime.



Figure 39. *Leucobryum juniperoideum*, one of the representatives of **Leucobryaceae** in Indonesia. Photo by Jan-Peter Frahm, with permission.



Figure 40. *Aerobryopsis wallichii*, one of the representatives of **Meteoriaceae** in Indonesia. Photo by Jan-Peter Frahm, with permission.



Figure 41. *Neckeropsis lepineana*, one of the representatives of **Neckeraceae** in Indonesia. Photo by Colin Meurk, through Creative Commons.



Figure 42. *Pterobryon* sp. (**Pterobryaceae**), a genus with the more robust species found in drier forests of tropical Asia. Photo by Efraín de Luna, with permission.



Figure 43. *Thuidium cymbifolium* with capsules, one of the representatives of **Thuidiaceae** in Indonesia. Photo by Li Zhang, with permission.



Figure 44. *Herbertus bivittatus* from the Neotropics. The family **Herbertaceae** is known in Indonesia. Photo by Michael Lüth, with permission.



Figure 45. *Mastigophora woodsii*. The family **Mastigophoraceae** is known in Indonesia. Photo by Blanka Agüero, with permission.



Figure 46. *Scapania compacta*; *S. javanica* represents the family **Scapaniaceae** in Indonesia. Photo by Michael Lüth, with permission.



Figure 47. *Gottschelia schizopleura*, one of the representatives of **Schistochilaceae** in Indonesia. Photo by Li Zhang, with permission.

Based on investigations in Southeast Asia, Africa, and South America, as the mountain vegetation zones shift from submontane to lower montane, the bryophyte life forms also shift (Kürschner *et al.* 1999). The **mats** are replaced by **fan** and **weft** formers that are able to take advantage of the cooler air with higher humidity. **Perennial stayers** and **perennial shuttle species** have a greater reliance on asexual propagules and clonal growth. The plants furthermore have a structure that permits them to take advantage of water vapor from fog, to conduct water internally, and to store water.

Lower Montane

In the lowland forest and the lower montane rainforest of Colombia (Figure 48), Wolf (1993a) identified four main bryophyte community groupings, primarily related to position within the host tree:

1. Communities of the lowland forest at 1,000 m (valley floor)
2. Communities of the lower montane rainforest, 1,250 m to ca. 2,130 (2,550) m
3. Communities of the upper montane rainforest, ranging from ~2,460 m to the treeline at 3,700 m.
4. Communities of *Polylepis* (Figure 49-Figure 50) dwarf forest at 4,130 m.



Figure 48. Lower montane forest in Colombia, rich in tracheophytic epiphytes. Photo by A. M. Cleef, courtesy of S. Robbert Gradstein.



Figure 49. Páramo of Ecuador with remnant subalpine *Polylepis* dwarf forest in the back at skyline. Photo courtesy of S. Robbert Gradstein.



Figure 50. Subalpine dwarf mossy *Polylepis pauta* forest in Ecuador. Photo by K. Romolero, courtesy of S. Robbert Gradstein.

The *Polylepis pauta* (Figure 49-Figure 50) forests have dominated in many humid environments of the high Andes of Ecuador, Peru, and Bolivia (3,500–4,500 m asl) (Gradstein & León-Yáñez 2018). However, now these forests are greatly diminished due to replacement with grasslands for grazing. They have become one of the most threatened ecosystems in South America. Gradstein and León-Yáñez have documented the liverwort flora in the remnant forests in the páramo of Papallacta, Ecuador, finding 51 liverwort species. The forest floor and tree bases were nearly completely covered with bryophytes, in particular *Lepidozia auriculata* (see Figure 99) and the robust *Plagiochila* species *P. dependula*, *P. ensiformis*, *P. fuscolutea* (Figure 51), and *P. ovata*. The branches had abundant growths of *Frullania paradoxa* (see Figure 55), *Leptoscyphus hexagonus* (see Figure 28), *Plagiochila bifaria* (Figure 52), and *P. punctata* (Figure 53).



Figure 51. *Plagiochila fuscolutea*, a species of the forest floor in the high Andes. Photo by Jan-Peter Frahm, with permission.



Figure 52. *Plagiochila bifaria*, a species from the Azores and also of the forest floor in the high Andes. Photo by Jan-Peter Frahm, with permission.



Figure 53. *Plagiochila punctata*, a species of the forest floor in the high Andes. Photo by Stan Phillips, through public domain.

The secondary, semi-deciduous lowland forest is dominated by *Machaerium capote* (Figure 54) (Wolf

1993a). The epiphytes are characterized by the leafy liverworts *Frullania ericoides* (Figure 55) and *Radula tectiloba* (Figure 56), as well as various *Lejeuneaceae* (Figure 9). *Frullania ericoides* is a pantropical xerophytic species. The canopy is characterized by a lichen community of *Heterodermia albicans* (Figure 57)-*Trypethelium eluteriae* (Figure 58). The trunk, by contrast, is dominated by the pendent moss *Meteorium nigrescens* (Figure 22) and the leafy liverwort *Radula caldana* (see Figure 56). Exclusive taxa in this association are *Papillaria nigrescens*, *Radula caldana*, *Mastigolejeunea auriculata* (Figure 59), *Porella brasiliensis* (see Figure 60), and *Sematophyllum subpinnatum* (see Figure 21). This community occurs from the tree base up to the inner crown. Epiphytes are absent on the twiglets of the outer canopy.



Figure 54. *Machaerium capote*, the dominant species in the secondary, semi-deciduous lowland forest. Photo by Damon Salveo, through Creative Commons.



Figure 55. *Frullania ericoides*, an epiphyte in secondary, semi-deciduous lowland forests of the Neotropics. Photo by Blanka Aguero, with permission.



Figure 56. *Radula*; *R. tectiloba* is an epiphyte in secondary, semi-deciduous lowland forests and *R. caldana* is a species of the trunk in the lowland forests of the Neotropics. Photo by Michael Lüth, with permission.



Figure 59. *Mastigolejeunea auriculata*, a species on tree trunks in secondary, semi-deciduous lowland forests in the Neotropics. Photo by Blanka Aguero, with permission.



Figure 57. *Heterodermia albicans*, part of the lichen community that dominates the canopy of the secondary, semi-deciduous lowland forest. Photo by Bobby Hattaway, with online permission through DiscoverLife.



Figure 58. *Trypethelium eluteriae*, part of the lichen community that dominates the canopy of the secondary, semi-deciduous lowland forest. Photo by Harrie Sipman, through Creative Commons.



Figure 60. *Porella navicularis* on tree; *P. brasiliensis* is a species **pendent** on tree trunks in secondary, semi-deciduous lowland forests in the Neotropics. Photo from Botany website, UBC, with permission.

Because of the high humidity, every surface is potentially a bryophyte substrate. But these are also suitable substrata for other types of plants. Ingram and Nadkarni (1993) reported that the bryophytes formed only 5% of the epiphytic organic matter in a Neotropical lower montane forest where the dominant host was *Ocotea tonduzii* (see Figure 61). Flowering plants formed only 10% of the species biomass, with dead organic matter being the dominant portion at 60%.



Figure 61. *Ocotea cf. leucoxydon*, a species that is dominant in a Neotropical lower montane forest where bryophytes comprise only 5% of the epiphytic organic matter. Photo by Jens G. Rohwer, through Creative Commons.

The lower montane rainforest communities differ from those of the lowland forest (Wolf 1993a). Exclusive species include the leafy liverwort *Lejeunea flava* (Figure 62-Figure 63), the pendent moss *Squamidium nigricans* (see Figure 116), and the foliose lichen *Parmotrema subsumptum* (Figure 64). Three of the six identified communities of epiphytes [*Bryopteris filicina* (Figure 65) tree bole community, *Cheilolejeunea trifaria* (Figure 66) - *Schlotheimia acutifolia* var. *angustifolia* (see Figure 67) community, *Plagiochila fragilis* (see Figure 51-Figure 53) community from tree crowns] share the liverwort species *Cheilolejeunea rigidula* (see Figure 66), *Frullania caulisequa* (Figure 68), *Lejeunea laetevirens* (Figure 69), and the moss *Sematophyllum subpinnatum* (see Figure 21). Furthermore, *Cheilolejeunea rigidula* and *Lejeunea laetevirens* are exclusive to these three communities. In other communities, exclusive species include *Diplasiolejeunea pauckertii* (see Figure 70) in the *Diplasiolejeunea pauckertii* - *Brachiolejeunea laxifolia* community and *Squamidium nigricans* in the *Frullania arecae* (Figure 71) - *Frullanoides densifolia* (Figure 72) - *Squamidium nigricans* community. In the *Bryopteris filicina* (Figure 65) community, present in the range of 1,210 and 1,980 m asl on the lower parts of tree trunks and less commonly on steep inner branches in the lower canopy, *B. filicina* is exclusive, accompanied by the

liverworts *Cheilolejeunea rigidula* and *Lejeunea laetevirens*. The liverworts are closely appressed and grow intermixed with feather-shaped dendroid genera such as *Bryopteris*, *Neckeropsis* (Figure 41), and *Porotrichum* (Figure 114) that stand out for several centimeters as horizontal shelves. The *Cheilolejeunea trifaria* - *Schlotheimia acutifolia* var. *angustifolia* community occurs in the inner crowns of trees in the range of 1,210 to 1,980 m asl. This Columbian community shares *C. trifaria* and *Lopholejeunea subfusca* (Figure 73) with a lower trunk community of open secondary forests at 1,300 m asl in Malaysia (Kürschner 1990). The *Diplasiolejeunea pauckertii* - *Brachiolejeunea laxifolia* community occurs in the outer canopy at elevations primarily from 2,460 to 2,550 m asl.



Figure 62. *Lejeunea flava*, a species exclusively in the lower montane rainforest. Photo by Linda Phillips, through Creative Commons.



Figure 63. *Lejeunea flava* growing as an epiphyll and typical in the lower montane rainforest. Photo by Yang Jia-dong, through Creative Commons.



Figure 64. *Parmotrema subsumptum*, a lichen exclusively in the lower Neotropical montane rainforest. Photo through Creative Commons.



Figure 65. *Bryopteris filicina*, a species that forms a tree bole community of the Neotropical lower montane rainforest. Photo by Eliana Calzadilla, through Creative Commons.



Figure 66. *Cheilolejeunea trifaria*, part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. *Cheilolejeunea rigidula* also occurs in the crowns. Photo by Michael Lüth, with permission.



Figure 67. *Schlotheimia* sp., part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. Photo by Michael Lüth, with permission.



Figure 68. *Frullania caulisequa*, part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. Photo by Blanka Aguero, with permission.



Figure 69. *Lejeunea laetevirens*, part of the bryophyte community in tree crowns in the Neotropical lower montane rainforest. Photo by Scott Zona, through Creative Commons.



Figure 70. *Diplasiolejeunea brunnea* in Ecuador on leaf. Photo by Tamás Pócs, with permission.



Figure 73. *Lopholejeunea subfusca* epiphyllous on palm in Fiji. This species occurs in the lower trunk community of open secondary forests in Malaysia. Photo by Tamás Pócs, with permission.



Figure 71. *Frullania arecae*, a species exclusive to the *Frullania arecae* - *Frullanoides densifolia* - *Squamidium nigricans* community in the lower montane tropical rainforest. Photo by Juan Larrain, with permission.



Figure 72. *Frullanoides densifolia*, a species exclusive to the *Frullania arecae* - *Frullanoides densifolia* - *Squamidium nigricans* community in the lower montane tropical rainforest. Photo by Jan-Peter Frahm, with permission.

In the lower montane rainforest of Panama, water content of bryophytes experiences pronounced daily flux (Zotz *et al.* 1997). These low and high levels are more important in limiting CO₂ exchange than the low photon flux density (light level) during rainstorms. More than half of the fixed carbon was lost to respiration during the night. Lösch *et al.* (1994) contributed an additional study on the photosynthetic gas exchange of bryophytes from the tropical lowlands and mountain forests of Central Africa.

In a lower montane rainforest of New Guinea, Edwards and Grubb (1977) estimated the epiphytic biomass to be 2 t ha⁻¹. Unfortunately, the bryophyte component of this was not measured separately, but the role of the epiphytes and accumulated "soil" in the crowns contribute ca. 1 t ha⁻¹ of soil. Minerals are released slowly from this epiphytic mass accumulation, providing a reservoir of nutrients for the soils.

Upper Montane

As the lower montane transitions into the upper montane, the proportion of **cushion**, **short**, and **tall turf** life forms of **perennial stayers** and **perennial shuttle species** begin to predominate (Kürschner & Parolly 2005). And as the habitat becomes more open, the bryophytes often have a dense rhizoid tomentum and a central conducting strand, aiding in rapid water conduction.

In the ericaceous forest of the upper montane of the Rwenzori Mountains of Uganda (Figure 74), Pentecost (1998) studied the epiphytes on mature trees of *Phillipia* (Ericaceae). *Usnea* spp. (Figure 75) and other macrolichens dominate the upper canopy. In the lower canopy, large cushion-forming liverworts such as *Chandonanthus* (Figure 76), *Herbertus* (Figure 44, Figure 77), and *Plagiochila* (Figure 10, Figure 51-Figure 53) dominate. Pentecost concluded that light intensity and age of host tree controlled the distribution of the bryophytes and lichens. Using fallen trees, Pentecost identified 14 bryophyte species, along with 2 algae, 22 lichens, and 2 ferns. The biomass of these organisms was nearly 1 ton ha⁻¹ and comprised 10% of the above-ground standing crop. Bryophytes held 8% of the above ground nutrients, with concentrations of 10 kg ha⁻¹ of N, 1 of P, and 3 of K. This

forest was cool, with the temperature below the canopy ranging 4-9.5°C during the 10-day study period. The temperature increased slightly with canopy height. Evaporation below the canopy decreased significantly with increasing altitude from 2,300 to 3,600 m asl.



Figure 74. Rwenzori Mountains with *Denrosenecio adnivalis*. Photo by Agripio, through Creative Commons.



Figure 75. *Usnea*, a genus that occurs in the upper canopy of the ericaceous forest of the upper montane of the Rwenzori Mountains of Uganda. Photo through Creative Commons.



Figure 76. *Chandonanthus squarrosus*; *Chandonanthus* forms cushions in the lower canopy in Rwenzori Mountains of Uganda. Photo by David Tng, with permission.



Figure 77. *Herbertus aduncus*, in a genus that forms cushions in the lower canopy in Rwenzori Mountains of Uganda. Photo by Adolf Ceska, with permission.

Bizot *et al.* (1978) conducted one of the early studies on East African bryophytes, sampling in Ethiopia, Kenya, and the United Republic of Tanzania. They identified 96 liverwort and 211 moss species. They concluded that the Ethiopian Highlands are a part of the Afrotropical vegetation group. Here they found disjunct populations of *Garckea comosa* (see Figure 78) and *Aongstroemia julacea* (Figure 79).



Figure 78. *Garckea flexuosa*; *G. comosa* occurs as a disjunct in the Afromontane region. Photo by Manju C. Nair, through Creative Commons.



Figure 79. *Aongstroemia julacea*, a disjunct in the Afromontane region. Photo by Jan-Peter Frahm, with permission.

Kürschner (2003) expanded his studies of epiphytic bryophytes to Arabia. He described the associations *Leptodonto* (Figure 80) - *Leucodonetetum schweinfurthii* (see Figure 81) and *Orthotricho* (Figure 82)-*Fabronietum socotranae* (see Figure 83) from the Yemen escarpment mountains. These associations are typical in the monsoon-impacted *Juniperus procera* (Figure 84) and *Acacia origena* (Figure 85) woodland. The species of bryophytes are typically drought-tolerant Afromontane mosses, with *Orthotrichum diaphanum* (Figure 82) and *Syntrichia laevipila* (Figure 86) typifying the synusia. The drought-tolerant *Orthotricho-Fabronietum socotranae* (see Figure 83) is dominated by **cushions**, **short turf**, and **mat-forming**

perennial stayers that regularly produce capsules. The sunny sites, by contrast, have **tail** or **fan** pleurocarpous **perennial shuttle species** with large spores and either moderately low reproduction or more "generative" reproduction, in addition to liverworts. This grouping forms the subhumid *Leptodonto* (Figure 80) - *Leucodonetetum schweinfurthii* (see Figure 81).



Figure 80. *Leptodon smithii*; *Leptodon* is a characteristic epiphyte in sunny sites in Arabia. Photo by Michael Lüth, with permission.



Figure 81. *Leucodon sciuroides*; *L. schweinfurthii* is a characteristic epiphyte in sunny sites in Arabia. Photo by Hermann Schachner, through Creative Commons.



Figure 82. *Orthotrichum diaphanum*, a drought-tolerant Afromontane moss in Arabian *Acacia* and *Juniperus* woodland. Photo by Michael Lüth, with permission.



Figure 83. *Fabronia pusilla*; *F. sacrotrana* is a drought-tolerant Afromontane moss in Arabian *Acacia* and *Juniperus* woodland. Photo by Michael Lüth, with permission.



Figure 86. *Syntrichia laevipila*, a drought-tolerant Afromontane moss in Arabian *Acacia* and *Juniperus* woodland. Photo by Jonathan Sleath, with permission.



Figure 84. *Juniperus procera*, a species that is habitat for bryophytes in monsoon regions of Arabia. Photo by Plantsman, through Creative Commons.



Figure 85. *Acacia abyssinica* in Tanzania; *A. origina* is habitat for bryophytes in monsoon regions of Arabia. Photo by Guenther Eichhorn, through Creative Commons.

In the upper montane oak forests in the Cordillera de Talamanca of Costa Rica, Holz *et al.* (2002) found a large diversification of microhabitats and a high diversity of bryophytes. Liverworts (106 species) were slightly more numerous than mosses (100), with 1 hornwort in only 6 ha of forest. The researchers identified three main groups of microhabitats: forest floor, including tree bases, phyllosphere, and other epiphytic habitats. The forest floor was much richer in bryophyte species than in forests of lower elevation zones. These were distributed among tree bases (69 species), rotten logs (70), and soil (69) as the most species-rich habitats (Figure 87), heralding the greater light than that in lowland forests. Trunks (61 species), branches of the inner canopy (35), twigs of the outer canopy (14), and leaves of the understory (14) supported somewhat fewer species (Figure 87).

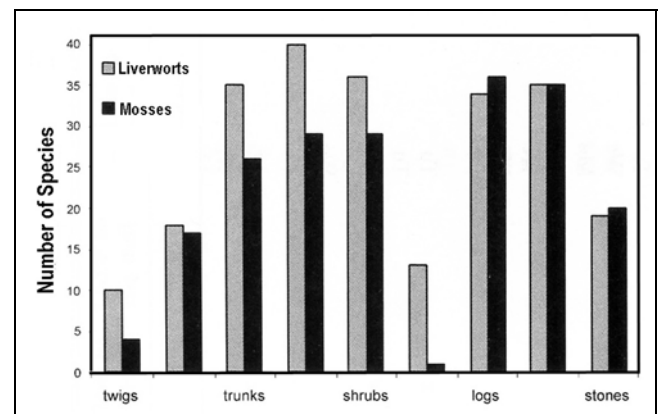


Figure 87. Number of species on each of the major microhabitats at Los Robles, Costa Rica, in the upper montane forest. Modified from Holz *et al.* 2002.

Holz and coworkers (2002) once again found that *Lejeuneaceae* (Figure 9) was by far the family represented by the most species, reaching ~60 at Monteverde, Costa Rica. The distribution of species among the major families is shown in Figure 88. The life forms are quite varied, with **turfs** and **mats** being the most common strategies (Figure 89). The "pronounced" dry season and host tree characters (tree height, stratification, number of host tree species)

modified this upper montane zone compared to more humid lower altitudes.

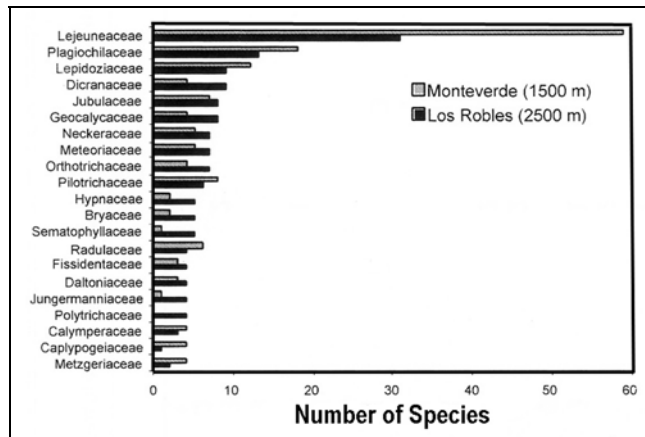


Figure 88. Numbers of species in the major bryophyte families in the upper montane forest at two sites in Costa Rica. Modified from Holz *et al.* 2002.

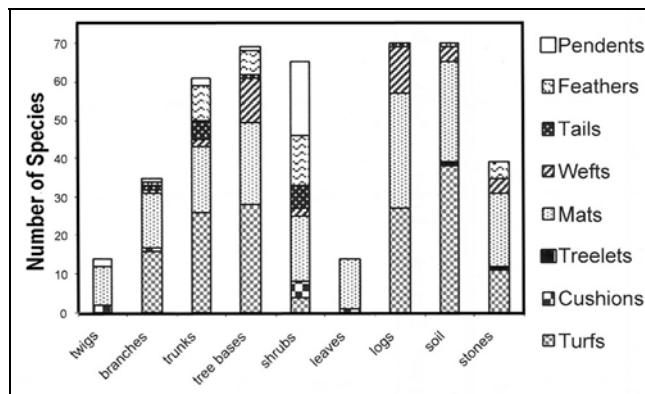


Figure 89. Proportions of species in each of the life forms in the major microhabitats at Los Robles, Costa Rica, in the upper montane forest. Modified from Holz *et al.* 2002.

Holz and Gradstein (2005) compared cryptogamic epiphytes in early and late secondary oak (*Quercus copeyensis*; Figure 90-Figure 91) forests and in primary forest in Cordillera de Talamanca, Costa Rica. They found little difference in species richness between the secondary and primary forests. They concluded that the closed canopy of the secondary forests explained the high diversity there, resulting at least in part from the high atmospheric humidity. Nevertheless, even after 40 years one-third of the primary forest species were still absent in the secondary forest. Furthermore, while diversity was similar, the community composition differed markedly between primary and secondary forest, with 40% of all the species restricted to the secondary forests.

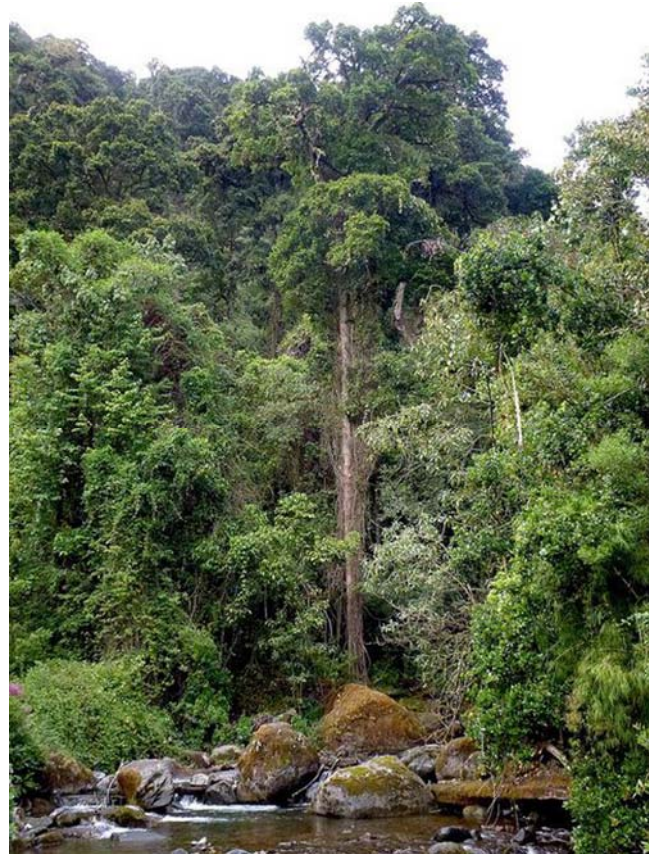


Figure 90. *Quercus copeyensis* forest like those in Cordillera de Talamanca, Costa Rica. Photo through Creative Commons.



Figure 91. *Quercus copeyensis*, a bryophyte host in Cordillera de Talamanca, Costa Rica. Photo through Creative Commons.

In the upper montane in the Central Cordillera of Colombia, rope-climbing techniques permitted assessment of the upper canopy (Wolf 1993b). Using the Braun-Blanquet method, Wolf sampled 15 sites at 200 m intervals on an altitudinal gradient. Wolf sampled four canopy trees, avoiding those with smooth, scaling, or hard bark. As in other studies, location within the host tree and altitude are the most influential characters on the epiphytic vegetation. Based on 59 host trees, Wolf found 187 liverwort and 108 moss species. There is great variability between relevés in

a single community, with a community of ~16%. A rapid change in community structure of the epiphytic vegetation occurs between 2,130 and 2,460 m asl. This is the elevation range where there is a rapid increase in air humidity. As in the Cordillera de Talamanca, *Usnea* (Figure 92) is very abundant in the outer canopy. pH values were somewhat wide-ranging and may have played a role in community composition. For example, at pH 7.1, the dominant community is that of the moss *Hypopterygium tamariscinum* (Figure 93) whereas at pH 3.2 the community of *Scapania portoricensis* (see Figure 46) – *Plagiothecium novogranatense* (see Figure 94–Figure 95) is prominent. The suspended soils of the lower montane rainforest and the upper montane rainforest differ significantly, with the latter having more organic matter and lower nutrient contents. Soils at tree bases in the lower montane rainforest have higher nutrient content than do the canopy soils. The opposite is the case in the upper montane rainforest. Exclusive epiphytic taxa in the upper montane rainforest are the liverworts *Adelanthus pittieri* (see Figure 96), *Bazzania breuteliana* (see Figure 97), *B. hookeri* (Figure 97), *Lepicolea pruinosa* (see Figure 98), *Lepidozia* spp. (Figure 99), *Lophocolea trapezoides* (see Figure 100), *Plagiochila bursata* (see Figure 10, Figure 51–Figure 53), *Riccardia* spp. (Figure 101), and *Trichocolea tomentosa* (Figure 102), and the moss *Sematophyllum insularum* (see Figure 21). In the canopy, the most common exclusive taxa are *Anoplolejeunea conferta*, *Jamesoniella rubricaulis* (Figure 103), *Leptoscyphus jackii* (see Figure 28), *L. porphyrius* (see Figure 28), *Plagiochila echinella*/*P. hansmeyeri*/*P. paludosa* (see Figure 10, Figure 51–Figure 53), *Prionodon fuscolutescens* (Figure 104), *Trachylejeunea dominicensis*, and the lichen *Hypotrachyna laevigata* (Figure 105)/*H. producta*. On tree bases, exclusive taxa for all five tree base communities include *Calypogeia peruviana* (Figure 106), *Cephalozia crassifolia* (Figure 107), *Lophocolea* aff. *connata* (see Figure 100), and *Telaranea nematodes* (Figure 108).



Figure 92. *Usnea* hanging on pine, an abundant species in the outer canopy at Cordillera de Talamanca, Costa Rica. Photo by Fährtenleser, through Creative Commons.



Figure 93. *Hypopterygium tamariscinum*, the dominant epiphytic community at pH 7.1 at Cordillera de Talamanca, Costa Rica. Photo by Efrain de Luna, with permission.



Figure 94. *Plagiothecium undulatum* on a rotting log. Photo from Botany Website, UBC, with permission.



Figure 95. *Plagiothecium dentatum*; some members of this genus occur at pH 3.2 on trees in Colombia. Photo by Janice Glime.



Figure 98. *Lepicolea ochroleuca*; *L. pruinosa* occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Jan-Peter Frahm, with permission.



Figure 96. *Adelanthus decipiens*; *A. pitteiri* occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Des Callaghan, through Creative Commons.



Figure 99. *Lepidozia cupressina*; some species in this genus occur exclusively as epiphytes in the upper montane rainforest of the Central Cordillera of Colombia. Photo from British Bryological Society, with permission per Barry Stewart.



Figure 97. *Bazzania hookeri*, a species that occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.



Figure 100. *Lophocolea cf polychaeta*; *L. trapezoides* occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.



Figure 101. *Riccardia fucoidea* from the Neotropics; several species of *Riccardia* occur exclusively as epiphytes in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.



Figure 102. *Trichocolea tomentella*, a widespread species that occurs exclusively as an epiphyte in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.



Figure 103. *Jamesoniella rubricaulis*, a species that occurs exclusively in the canopy in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Jan-Peter Frahm, with permission.



Figure 104. *Prionodon fuscolutescens*, a species that occurs exclusively in the canopy in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Juan David Parra, through Creative Commons.



Figure 105. *Hypotrachyna laevigata*, a lichen that occurs exclusively in the canopy in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Siri Synnøve Høle, through Creative Commons.



Figure 106. *Calypogeia peruviana*, one of the exclusive liverwort taxa for tree bases in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Paul Davison, with permission.

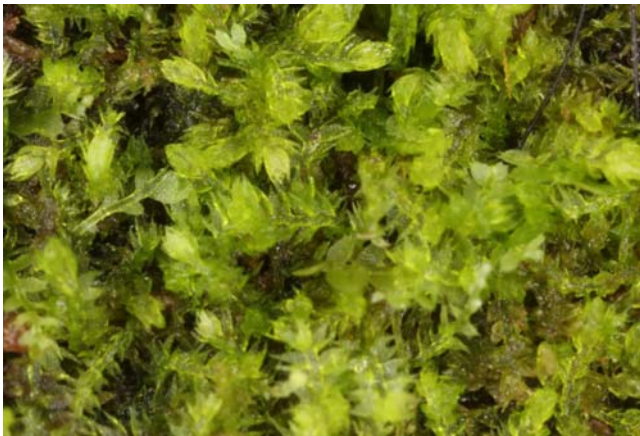


Figure 107. *Cephalozia crassifolia*, one of the exclusive liverwort taxa on tree bases in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Jan-Peter Frahm, with permission.



Figure 108. *Telaranea nematodes*, one of the exclusive liverwort taxa on tree bases in the upper montane rainforest of the Central Cordillera of Colombia. Photo by Michael Lüth, with permission.

The most common taxa exclusive for the canopy communities of the upper montane rainforest of the Central

Cordillera of Colombia are *Anoplolejeunea conferta*, *Jamesoniella rubricaulis* (Figure 103), *Leptoscyphus jackii* (see Figure 28), *L. porphyrius* (see Figure 28), *Plagiochila echinella sensu lato* (incl. *P. hansmeyerii* and *P. paludosa*; see Figure 10, Figure 51-Figure 53), *Prionodon fuscolutescens* (Figure 104), *Trachylejeunea dominicensis*, and *Hypotrachyna laevigata* (not separated from *H. producta*; Figure 105).

In Tanzania (Figure 109), the upper montane forest bryophytes capture 50% of the yearly precipitation (Gradstein 1992). That amount is 2.5 times the capture of the lower montane forest. Interception values in the Colombian montane forests were much less, reaching only 18.3% capture in the upper montane forest (Veneklaas & van Ek 1991). This difference is likely to be related to the differences in the forest types, with the Colombian mossy forest being much higher and much more open (Gradstein 1992). Furthermore, bryophytes in the Colombian forest formed discontinuous cover on the branches and usually were in clumps, contrasting with nearly continuous bryophyte cover on the branches in Tanzania.



Figure 109. Kilimanjaro at Amboseli National Park, Tanzania. Photo by Ninara, through Creative Commons.

The leafy liverwort genera *Plagiochila* (Figure 10, Figure 51-Figure 53), *Bazzania* (Figure 97), *Herbertus* (Figure 44, Figure 77), *Lepidozia* (Figure 99), *Lepicolea* (Figure 98), and *Trichocolea* (Figure 102) are the dominant liverworts in the wetter tropical montane forests (Gradstein 1992). In drier forests, mosses are more common. These include *Macromitrium* (Figure 110), *Meteoridium* (Figure 111), *Mittenothamnium* (Figure 112), *Papillaria* (Figure 113), *Porotrichum* (Figure 114), *Porotrichodendron*, *Prionodon densus* (Figure 115), and *Squamidium* (Figure 116). In Asia, one might find more robust mosses such as *Dicranoloma* (Figure 117), *Hypnodendron* (Figure 118), *Braunfelsia*, *Dicnemon* (Figure 119), and various members of the *Pterobryaceae* (Figure 42).



Figure 110. *Macromitrium sulcatum*; some members of *Macromitrium* occur in dry tropical forests on *Careya arborea*. Photo by Shyamal L., through Creative Commons.



Figure 113. *Papillaria flavolimbata*; the genus *Papillaria* is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Lorraine Phelan, through Creative Commons.



Figure 111. *Meteoridium remotifolium*; the genus *Meteoridium* is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Michael Lüth, with permission.



Figure 114. *Porotrichum bigelowii*; the genus *Papillaria* is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Michael Lüth, with permission.



Figure 112. *Mittenothamnium reptans* from the Neotropics; the genus *Mittenothamnium* is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Michael Lüth, with permission.



Figure 115. *Prionodon densus*, a species among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Jan-Peter Frahm, with permission.



Figure 116. *Squamidium* sp., a genus that is among the dominant liverworts in the drier montane forests of the Neotropics. Photo by Janice Glime.



Figure 117. *Dicranoloma billardierei*, in a genus with the more robust species found in drier forests of tropical Asia. Photo by Juan Larrain, with permission.



Figure 118. *Hypnodendron menziesii*, in a genus with the more robust species found in drier forests of tropical Asia. Photo by Jan-Peter Frahm, with permission.

Upper montane forests can have epiphytic bryophyte biomass reaching as much as 44 tons dry weight per hectare (Gradstein 1992), compared to only ~2 tons in the submontane rainforest (Pócs 1982).

Gradstein and Vána (1994) reported that rotten logs in the pine forests in the central highlands of Chiapas, Mexico, exhibited a *Nowellia curvifolia* (Figure 23) community that had many species of boreal liverworts. They found eight species of liverworts and two of mosses. The most abundant of these, forming dense mats, were the leafy liverworts *Fuscocephaloziopsis catenulata* (Figure 120) and *Nowellia curvifolia* and the mosses *Campylopodia stenocarpa* and *Dicranum frigidum* (Figure 26). Other common species were the liverworts *Syzygiella autumnalis* (Figure 121), *Leptoscyphus amphibolus* (see Figure 122), and *Lophozia ventricosa* (Figure 123), with *Crossocalyx hellerianus* (Figure 124) often occurring on the very humid flanks of the logs. The species were all pioneers on the logs except for *Dicranum frigidum*. Six of the liverwort species are characteristic of boreal forest conifer logs. The researchers concluded that this community is probably limited in the tropics to occurrences of conifer forests in the northern parts of Central America.



Figure 119. *Dicnemon calycinum* with capsules, in a genus with the more robust species found in drier forests of tropical Asia. Photo by Janice Glime.



Figure 120. *Fuscocephaloziopsis catenula*, a species that forms dense mats on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by H. Tinguy, National Museum of Natural History, with online permission.



Figure 121. *Syzygiella autumnalis*, a species that forms dense mats on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by H. Tinguy, French National Museum of Natural History, with online permission.



Figure 124. *Crossocalyx hellerianus*, a common species on the flanks of rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by Štěpán Koval, with permission.



Figure 122. *Leptoscyphus azoricus*; *L. amphibolius* is a common species on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by Jan-Peter Frahm, with permission.



Figure 123. *Lophozia ventricosa*, a common species on rotten logs in the pine forests in the central highlands of Chiapas, Mexico. Photo by Hermann Schachner, through Creative Commons.



Figure 125. *Cupressus lusitanica*; the greatest diversity of bryophytes is in the plantations of these species. Photo by Sergio Kasusky, through Creative Commons.

Corrales *et al.* (2010) surveyed secondary montane forest, *Cupressus lusitanica* (Figure 125) plantations, and *Pinus patula* (Figure 126) plantations in the Central Cordillera of Colombia. They used 1 m² random plots along 40 transects. They identified 151 species of bryophytes. Species richness, weighted based on number of samples, was higher in the secondary montane forests and cypress plantations than in the pine plantations. The greatest abundance was in the cypress plantations. Nevertheless, DCA indicated a high degree of floristic similarity. Soil pH, slope, and light availability were the primary factors in determining bryophyte distribution, suggesting that habitat specialization is the main mechanism governing species distribution within a forest type. The similarity of the three forest types suggests that propagule dispersal is also important.



Figure 126. *Pinus patula*; plantations of this species have fewer bryophyte species than those of the cypress (*Cupressus lusitanica*). Photo by Dick Culbert, through Creative Commons.

Veneklaas *et al.* (1990) investigated the effects of epiphytic vegetation in rainfall interception in an upper montane rainforest at 3,370 m asl in the Central Cordillera of the Colombian Andes. This site had ~12 tons dry weight of epiphytes per hectare, comprised mostly of bryophytes and dead organic matter. They learned that the epiphytes were efficient at rainfall capture, gradually releasing the excess. Furthermore, loss through evaporation was slow.

Summary

High mountains throughout the tropics have similar zonation patterns. Canopy tree presence or absence are important determinants of the bryophyte vegetation. Water relations are important, and trees affect the relative humidity. Nitrogen is made available by associated **Cyanobacteria** species. Submontane species are primarily **mat-forming perennial stayers** and **perennial shuttle species**. Liverworts outnumber mosses in humid areas, but the reverse is true in dry areas. Montane regions often have rocky substrata as well as soil, contributing to niche diversity. The montane is also likely to have more temperate plants than the submontane. These regions contrast sharply with the lowland forests by having dense carpets of bryophytes on the forest floor. Trees often support **pendent** bryophytes, and **tall turfs** and **feathers** are common. These more favorable growing conditions support some of the richest diversity of bryophytes in the world and the most exclusive species.

Lejeuneaceae can dominate in all the epiphytic zones. **Meteoriaceae** dominates in montane forests, with **Dicranaceae** typically dominant in the upper montane. The bryophyte communities of the montane have considerable similarity to those of the boreal zones. Bryophytes on logs are predominately liverworts.

Bryophytes lost through disturbances can be replaced through diaspore banks, with liverworts more common than mosses. In the lower montane, water content experiences pronounced daily fluxes. Much carbon is still lost due to respiration at night. Soils at tree bases in the lower montane have higher nutrient content than do the canopy soils. The upper montane bryophytes of Tanzania capture 50% of the precipitation, 2.5 times that captured in the lower montane, but Neotropical bryophytes can be in discontinuous clumps and capture much less water. Upper montane forests can have as much as 44 tons of bryophyte biomass, compared to only 2 in submontane forests. In the upper montane, **cushion**, **short**, and **tall turf** life forms increase in proportion among the typically **perennial stayers** and **perennial shuttle species**.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about.

Literature Cited

- Acebey, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.
- Benítez, Á, Prieto, M., and Aragón, G. 2015. Large trees and dense canopies: Key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. *Forestry* 88: 521-527.
- Bisang, I., Piipo, S., and Hedenäs, L. 2003. Bryophyte diaspore bank in three Malaysian mountain rainforests. *J. Bryol.* 25: 68-70.
- Bizot, M., Friis, I., Lewinsky, J., and Pócs, T. 1978. East African bryophytes IV. Danish collections. *Lindbergia* 4: 259-284.
- Churchill, S. P., Balslev, H., Forero, E., and Lutey, J. L. (eds.). 1995. Biodiversity and Conservation of Neotropical Montane Forests. New York Botanical Garden, N. Y.
- Churchill, S. P., Sanjines, A. N., and Aldana, M. C. 2009. Catálogo de los briofitas de Bolivia: diversidad, distribución y ecología. Santa Cruz de la Sierra: Museo de Historia Natural Noel Kempff Mercado and Missouri Botanical Garden.
- Corrales, A., Duque, A., Uribe, J., and Londoño, V. 2010. Abundance and diversity patterns of terrestrial bryophyte species in secondary and planted montane forests in the northern portion of the Central Cordillera of Colombia. *Bryologist* 113: 8-21.
- Costa, D. P. and Lima, F. M. 2005. Moss diversity in the tropical rainforests of Rio de Janeiro, southeastern Brazil. *Rev. Brasil. Bot.* 28: 671-685.

- Costa, D. P., Santos, N. D., Rezende, M. A., Buck, W. R., and Schäfer-Verwimp, A. 2015. Bryoflora of the Itatiaia National Park along an elevation gradient: Diversity and conservation. *Biodiv. Conserv.* 24: 2199-2212.
- Dauphin L., G. and Grayum, M. H. 2005. Bryophytes of the Santa Elena Peninsula and Islas Murciélagos, Guanacaste, Costa Rica, with special attention to Neotropical dry forest habitats. *Lankesteriana* 5(1): 53-61.
- DeWalt, S. J., Ickes, K., and James, A. 2016. Forest and community structure of tropical sub-montane rain forests on the island of Dominica, Lesser Antilles. *Caribb. Nat. Spec. Iss. No. 1*: 116-137.
- Edwards, P. J. and Grubb, P. J. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. *J. Ecol.* 65: 943-969.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Gradstein, S. R. 1992. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 234-258.
- Gradstein, S. R. 1995. Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). *Biodiversity and conservation of Neotropical montane forests*. New York Botanical Garden, Bronx, N. Y., pp. 321-334.
- Gradstein, S. R. and Culmsee, H. 2010. Bryophyte diversity on tree trunks in montane forests of Central Sulawesi, Indonesia. *Trop. Bryol.* 31: 95-105.
- Gradstein, S. R. and León-Yáñez, S. 2018. Liverworts (Marchantiophyta) of *Polylepis pauta* forests from Ecuador with description of *Leptoscyphus leoniae* sp. nov. and *Plagiochila pautaphila* sp. nov. *Nova Hedw.* 106: 35-48.
- Gradstein, S. R. and Vána, J. 1994. A boreal bryophyte community in a tropical montane forest of Mexico. *Trop. Bryol.* 9: 31-34.
- Gradstein, S. R., Reenen, G. B. A. van, and Griffin, D. III. 1989. Species richness and origin of the bryophyte flora of the Colombian Andes. *Acta Bot. Neerl.* 38: 439-448.
- Grubb, P. J. 1977. Control of forest growth and distribution on wet tropical mountains: With special reference to mineral nutrition. *Ann. Rev. Ecol. Syst.* 8: 83-107.
- Grubb, P. J., Lloyd, J. R., Pennington, T. D., and Whitmore, T. C. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy and floristics. *J. Ecol.* 51: 567-601.
- Holz, I. and Gradstein, S. R. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. *Plant Ecol.* 178: 89-109.
- Holz, I., Gradstein, S. R., Heinrichs, J., and Kappelle, M. 2002. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. *Bryologist* 105: 334-348.
- Hylander, K., Pócs, T., and Nemomissa, S. 2010. Liverworts of southwest Ethiopian montane forests: ecological and biogeographical notes. *J. Bryol.* 32: 92-100.
- Ingram, S. W. and Nadkarni, N. M. 1993. Composition and distribution of epiphytic organic matter in a Neotropical cloud forest. *Selbyana* 14: 37-45.
- Kürschner, H. 1990. Die epiphytischen Moosgesellschaften am Mt. Kinabalu (Nord-Borneo, Sabah, Malaysia). *Nova Hedw.* 51: 1-75.
- Kürschner, H. 2003. Epiphytic bryophyte communities of southwestern Arabia – phytosociology, ecology and life strategies. *Nova Hedw.* 77: 55-71.
- Kürschner, H. and Parolly, G. 2005. Ecosociological studies in Ecuadorian bryophyte communities III. Life forms, life strategies and ecomorphology of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedw.* 80: 89-113.
- Kürschner, H., Frey, W., and Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – A pantropical synopsis. *Nova Hedw.* 69: 73-99.
- Linares, E. L. 1986. Estudio taxonomico y ecologico de la brioflora en la franja alto andina de "El Tabalzo," Cundinamarca. [Taxonomic and ecological study of the bryoflora in the high Andean strip of "El Tabalzo," Cundinamarca.]. Ph.D. Thesis, Universidad Nacional de Colombia, Bogotá, 308 pp.
- Lösch, R., Mülders, P., Fischer, E., and Frahm, J.-P. 1994. Photosynthetic gas exchange of bryophytes from tropical lowland and mountain forests of eastern Central Africa. *Trop. Bryol.* 9: 169-186.
- Parolly, G. and Kürschner, H. 2004. Ecosociological studies in Ecuadorian bryophyte communities. II. Syntaxonomy of the submontane and montane epiphytic vegetation of S Ecuador. *Nova Hedw.* 79: 377-424.
- Pentecost, A. 1998. Some observations on the biomass and distribution of cryptogamic epiphytes in the upper montane forest of the Rwenzori Mountains, Uganda. *Global Ecol. Biogeogr. Lett.* 7(4): 273-284.
- Pires, J. M. and Prance, G. T. 1985. The vegetation types of the Brazilian Amazon. Chapt. 7. In: Prance, G. T. and Lovejoy, E. T. (ed.). *Key Environments: Amazonia*. Pergamon Press, Oxford, pp. 109-145.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 59-104.
- Romanski, J., Pharo, E. J., and Kirkpatrick, J. B. 2011. Epiphytic bryophytes and habitat variation in montane rainforest, Peru. *Bryologist* 114: 720-731.
- Song, L., Ma, W.-Z., Yao, Y.-L., Liu, W.-Y., Li, S., Chen, K., Lu, H.-Z., Cao, M., Sun, Z.-H., Tan, Z.-H., and Nakamura, A. 2015. Bole bryophyte diversity and distribution patterns along three altitudinal gradients in Yunnan, China. *J. Veg. Sci.* 26: 576-587.
- Sonnleitner, M., Dullinger, S., Wanek, W., and Zechmeister, H. 2009. Microclimatic patterns correlate with the distribution of epiphyllous bryophytes in a tropical lowland rain forest in Costa Rica. *J. Trop. Ecol.* 25: 321-330.
- Sporn, S. G., Bos, M. M., Kessler, M., and Gradstein, S. R. 2010. Vertical distribution of epiphytic bryophytes in an Indonesian rainforest. *Biodiv. Conserv.* 19: 745-760.
- Valdevino, J. A., Sá, P. S. A., and Pôrto, K. C. 2002. Musgos pleurocárpicos de mata serrana em Pernambuco, Brasil Pleurocarpous mosses of a sub-montane rain forest in Pernambuco State, Brazil. *Acta Bot. Brasil.* 16: 161-174.
- Veneklaas, E. J. 1990. Nutrient fluxes in bulk precipitation and throughfall in two montane tropical rainforests, Colombia. *J. Ecol.* 78: 974-992.
- Veneklaas, E. J. and Ek, R. van. 1991. Rainfall interception in two tropical montane rain forests, Colombia. *Hydrol. Process.* 4: 311-326.

- Veneklaas, E. J., Zagt, R. J., Leerdam, A. van, Ek, R. van, Brockhoven, A. J., and Genderen, M. van. 1990. Hydrological properties of the epiphyte mass of a montane tropical forest, Colombia. *Vegetatio* 89: 183-192.
- Wolf, J. H. D. 1993a. Epiphyte communities of tropical montane rain forest in the northern Andes. I. Lower montane communities. *Phytocoenologia* 22: 1-52.
- Wolf, J. H. D. 1993b. Epiphyte communities of tropical montane rainforest in the northern Andes II. Upper montane communities. *Phytocoenologia* 22: 53-103.
- Zotz, G., Büde, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO₂ exchange of tropical bryophytes in a lower montane rainforest in Panama. *Bot. Acta* 110: 9-17.

CHAPTER 8-10

TROPICS: CLOUD FORESTS, SUBALPINE, AND ALPINE

TABLE OF CONTENTS

Cloud Forests	8-10-2
Adaptations and Water Relations.....	8-10-2
Biomass.....	8-10-5
Colonization and Life Strategies.....	8-10-7
Species Diversity	8-10-8
Mount Kenya	8-10-21
Lowland Cloud Forest.....	8-10-22
Role.....	8-10-23
Subalpine.....	8-10-25
Alpine.....	8-10-25
Páramo	8-10-28
Moss Balls	8-10-31
Afro-alpine.....	8-10-33
Summary	8-10-38
Acknowledgments.....	8-10-39
Literature Cited	8-10-39

CHAPTER 8-10

TROPICS: CLOUD FORESTS, SUBALPINE, AND ALPINE



Figure 1. Ecuadorian mountains and cloud forest. Photo by Arthur Anker, with permission.

Cloud Forests

Neotropical **cloud forests** (Figure 2, often known as **elfin forests** or **mossy forests**, extend from 23°N to 25°S (Churchill *et al.* 1995). These researchers suggested that the cloud forests of the Neotropics are a subset of the montane rainforest. They are isolated in Mexico on the north by xeric vegetation and on the south in Chile and Argentina by temperate rainforest. These cloud forests generally occur at 1000-3000 m asl. But the seasonal variation in precipitation is low and there are no months in which the evapotranspiration exceeds the rainfall. Rather, cloud cover is nearly continuous, with 2,000-4,000 mm precipitation per year. The temperature decreases from 18-22°C at 1,000 m to less than 10°C at 3,000 m asl. The taxa of these cloud forests are strongly influenced by their connections with both North and South America. The low generic level of endemism and high species endemism suggest recent and rapid speciation.



Figure 2. Cloud forest at Parque Nacional Montaña de Santa Bárbara at 2,180 m asl in Honduras. Photo by Josiah Townsend, with permission.

Cloud forests carry an intrigue that matches their names. Generally perched atop high mountains where they are blanketed in the fog of low-lying clouds or recipients of moisture-laden air that results in a mist zone most of the time (Vitt 1991), these forests must survive the harsh, uninterrupted winds and the continuous moisture that accompanies such a lofty abode. (See also Lawton 1980, 1982.) Consequently, trees there tend to be short compared to forests at lower elevations. For example, in Taveuni, Fiji, the forest trees on top of Mt. Koroturanga at 1,210 m asl were about 3-7 m tall, increasing to 10 m at 1,140 m elevation, and to 30 m at sea level (Ash 1987). Sadly, these dwarfed forests are rapidly disappearing from the face of the Earth before we can begin to understand a fraction of their complexity. In the northern Andes alone, 90% of these remarkable forests have disappeared, compared with 20% loss of the Amazon rainforest (Wuethrich 1993). In Peru alone, the mountainous areas house more than 25,000 plant species.

One problem that keeps these elfin forests out of the public eye is their relative lack of trees. Instead, they are dominated by herbs, shrubs, epiphytic ferns and seed plants, and mosses, with the diversity of all of these increasing with altitude (Wuethrich 1993). Nevertheless, they are the source of more than 3,000 species of plants that are used by the local people and house the ancestors of some of the most important world food crops.

Gotsch *et al.* (2017) showed that vapor pressure deficit could predict the epiphyte abundance in a tropical elevational gradient where the montane cloud forests occupy only a narrow band of microclimate and are thus vulnerable to climate change that changes the heights of the clouds and brings drought to the area. Their predictions are supported by their data showing that epiphyte abundance increases with elevation and leaf wetness and that it decreases as vapor pressure deficit (VPD) increases. VPD differences, however, are not always correlated with elevation and thus serve as better predictors of the epiphyte abundance.

In cloud forests of the Amazon, a high density of 21,900 trees per hectare belies the low tree species richness of 15 species, whereas the lower elevation tabonuco has 170 species with only 1750 trees per hectare (Gorchov & Cornejo 1993). The area behaves as an **ombrotrophic** (low-nutrient) wetland with its 5000 mm rainfall per year and another 10% moisture contributed by clouds. Poor soil oxygenation due to water logging results in most roots being above the soil. These buttress roots are usually covered by numerous bryophytes, and one might suppose that these bryophytes steal most of the nutrients returned by stemflow. Research has begun only recently on the ecological role of these cloud forest bryophytes.

Terrestrial bryophyte cover in the elfin forest is strikingly different from that of the lowland rainforest. The bryophytes are less specialized, with many of the same taxa occurring on the soil and on the trees. And the higher moisture permits bryophytes to grow higher on the bole, often reaching the canopy (Richards 1984).

Russell and Miller (1977) found that at Pico del Oeste in Puerto Rico, 55% of their collections of *Campylopus* (Figure 3) also contained the moss *Hemiragis* (Figure 4), but *Hemiragis* never occurred with *Leucoloma* (Figure 5). As in the submontane rainforest, the leafy liverworts

dominated the upper branches (Russell & Miller 1977). This high humidity no doubt accounts for the high percentage of leafy liverworts, estimated up to 90% of the bryophyte flora (Fulford *et al.* 1970). Yet at Monteverde, Costa Rica, Gradstein *et al.* (2001b) found that 36% of the 190 bryophyte species occurred exclusively in the canopy. The thick, lower branches had the highest diversity, with 99 species, presenting a sharp delineation of communities (Figure 6).



Figure 3. *Campylopus introflexus*, in a genus that occurs in the Pico del Oeste cloud forest in Puerto Rico. Photo by Paul Wilson, with permission.



Figure 4. *Hemiragis aurea*, in a genus that occurs in the Pico del Oeste cloud forest in Puerto Rico. Photo by Elisabeth Lavocat Bernard, with permission.



Figure 5. *Leucoloma* from the Neotropics, a genus that never occurs with *Hemiragis* in the cloud forest. Photo by Michael Lüth, with permission.

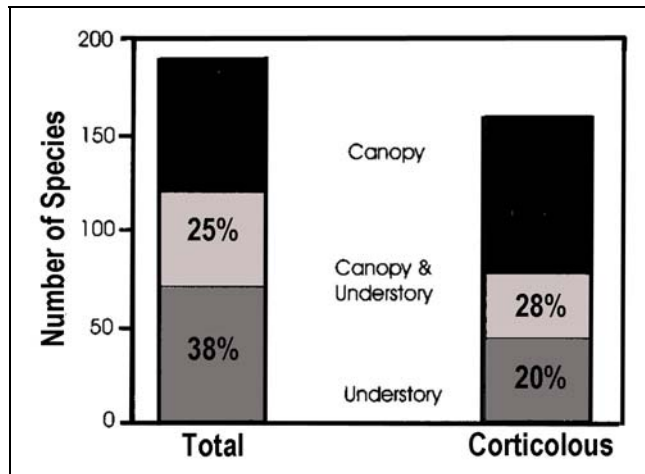


Figure 6. Total bryophyte species richness vs corticolous bryophyte species diversity in the canopy vs the understory in a cloud forest at Monteverde, Costa Rica. Species of rotten logs and epiphylls are not included in the corticolous counts. Redrawn from Gradstein *et al.* 2001b.

Merwin *et al.* (2001) reported 198 epiphytic bryophyte taxa in the Monteverde Cloud Forest Preserve. As is typical, the liverwort species (120) considerably outnumbered the moss species (77), with only 1 hornwort. Of these bryophyte species, 63 occurred in secondary forest and 84 in pastureland, whereas 178 species occurred in the primary forest.

These forests have such dense bryophyte growths on every trunk, branch, and twig that the forests appear "furry" (Gradstein & Pócs 1989). Biomass is high, with 11,000 kg ha⁻¹ dry weight in a Tanzanian elfin forest (80% of total canopy biomass), compared to the lower submontane rainforest with 1,773 kg (Pócs 1982). By comparison, an oak forest in Atlantic Europe had 355 kg (Schnock 1972) and a continental European oak forest had only 41 kg (Simon 1974).

One can find accumulations of organic matter in the crowns of trees of tropical wet forests such as the cloud forests. Bohlman *et al.* (1995) investigated the moisture and temperature patterns of these organic soils in the canopy and on the ground in Costa Rica. These two soil groupings ranged in temperature from 11.5°C to 21.0°C throughout the 42-month study period, but the soil from the two locations generally were within 1°C of each other. Both soils remained moist (>70% water content) during the wet and misty seasons. Nevertheless during dry periods the canopy soils dropped to a water content of 20-40% while the forest floor soils retained 60-70% water content.

Gotsch *et al.* (2016) considered that a shift in the heights of the cloud base or precipitation due to climate change would make a huge impact on the cloud forest epiphyte community.

For a more general understanding of cloud forests one can consult such publications as that of Stadtmüller (1987).

Adaptations and Water Relations

In two Venezuelan cloud forests (Figure 7) in the northern Andes at 2000-2400 m, rainfall in January and February is typically 20 mm or less, but in August to October it can be 200 mm or more (León-Vargas *et al.* 2006). Nevertheless, it is quite variable in all seasons. The longest record for a dry period is only 143 hours. Humidity

typically rises to more than 90% relative humidity at night, with one night in two typically reaching 100%. Six **pendent** (Figure 16) bryophytes were all able to survive at least a few days of desiccation; their recover was, however, better from high humidities. Their ability to reach light-saturation reached 95% at 110-256 $\mu\text{mol m}^{-2} \text{s}^{-1}$, levels only slightly higher than that of typical field levels. The **pendent** and other diffuse life forms are especially able to intercept cloudwater droplets, a feature that permits them to maximise conditions during periods of low rainfall.



Figure 7. Cloud forests, Venezuelan Andes. Photo by Gianfranco Cardogna, through Creative Commons.

The horizontal plane of a **fan** provides maximum surface area to capture light for photosynthesis as well as intercepting water from the moving air (Song *et al.* 2015). In three of the common **fan** bryophytes [moss *Homaliodendron flabellatum* (Figure 8), liverworts *Plagiochila arbuscula* (Figure 9), *P. assamica*] in an Asian subtropical montane cloud forest, the plants experienced high relative humidity coupled with low light and temperatures in the understory. Fog is a major source of water. Data suggest that photosynthetically active periods for these bryophyte are short because they lose most of their free water within an hour. These **fan** bryophytes are further adapted to their low-light understory position by having low light saturation and compensation points for photosynthesis. The researchers expressed concern that these **fan** bryophytes would experience a net carbon loss if the frequency and severity of dry periods increase.



Figure 8. *Homaliodendron flabellatum*, a **fan** form found in the Asian subtropical montane cloud forest. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.



Figure 9. *Plagiochila arbuscula*, a **fan** life form found in the Asian subtropical montane cloud forest. Photo by Peter de Lange, through public domain.

In the Asian subtropical montane cloud forest, there is high relative humidity accompanied by low light levels and temperatures in the understory (Song *et al.* 2015). Fog provides good water availability for the bryophytes. In this habitat, **fan** life forms (Figure 8-Figure 9) thrive. This life form loses its free water within one hour. Without sufficient water content, net photosynthesis can become negative. Song *et al.* (2015b) considered the **fan** life form to be especially suited to the cloud forest regime. The **fan** life form, extending outward from the vertical surfaces of trees (or rocks), is able to capture water from fog efficiently (Song *et al.* 2015). Furthermore, the cell walls have a high elasticity and osmoregulatory capacity that permit these life forms to tolerate desiccation. Additionally, these **fan** species have low light saturation and low compensation points for photosynthesis, all providing shade tolerance. While these characteristics provide ideal adaptations to the humid, low-light conditions of the cloud forest, the inability to tolerate and succeed under desiccating conditions puts these **fan** species at risk under changing climatic conditions that increase both the frequency and severity of droughts.

Biomass

Van Dunne and Kappelle (1998) estimated biomass of epiphytic bryophytes on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. They found 22 species each of mosses and liverworts. Biomass of bryophytes was correlated with frequency, with mosses contributing 54-99% of that biomass. Of these, 14% of the species accounted for 90% of the biomass. These bryophytes are important in controlling water flow. Dominant taxa include *Pilotrichella flexilis* (Figure 11), *Rigodium* sp. (Figure 12), *Porotrichodendron superbum* (Figure 13), *Prionodon densus* (Figure 14), *Neckera chilensis* (see Figure 15), and *Plagiochila* (Figure 16).

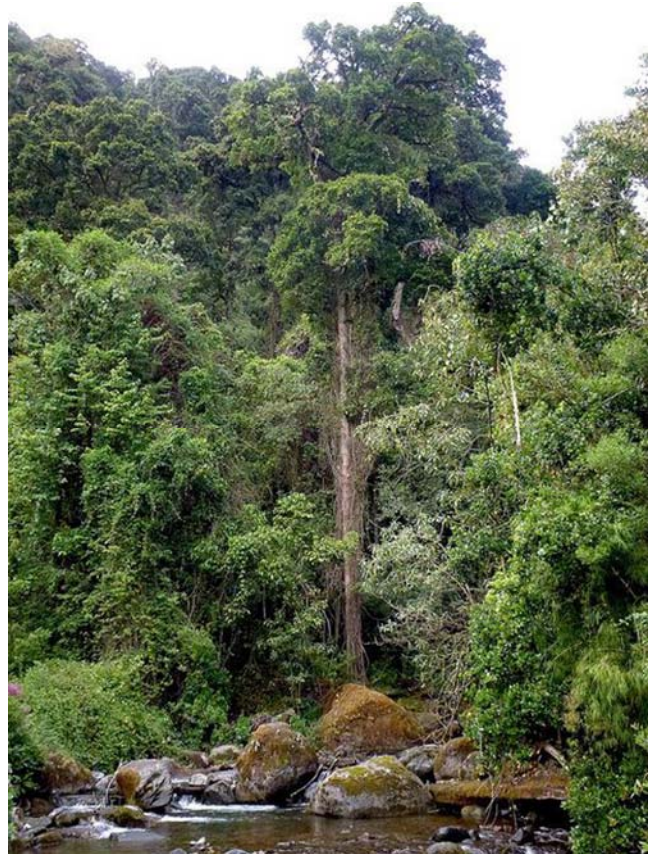


Figure 10. *Quercus copeyensis*, a good bryophyte substrate in a Costa Rican montane cloud forest. Photo through Creative Commons.

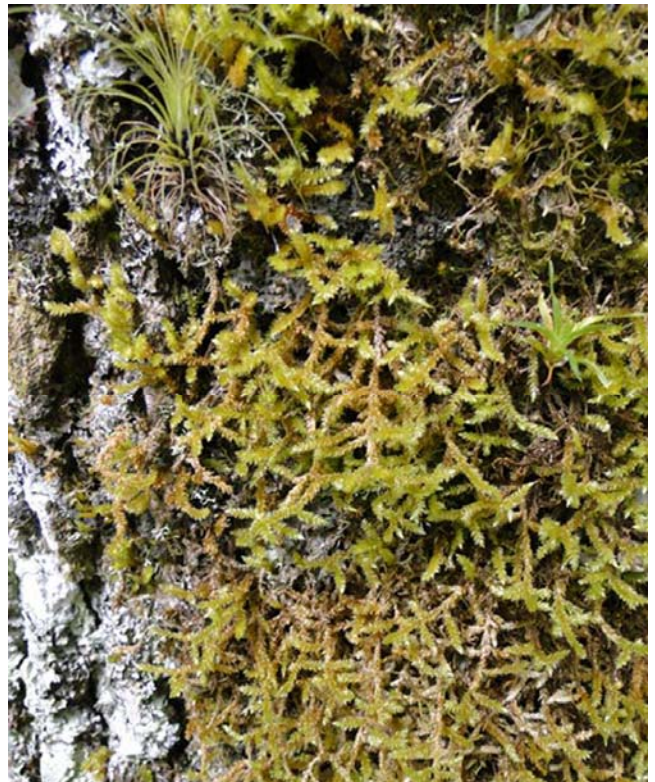


Figure 11. *Pilotrichella flexilis*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Claudio Delgadillo Moya, with permission.



Figure 12. *Rigodium pseudo-thuidium*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Juan Larrain, through Creative Commons.

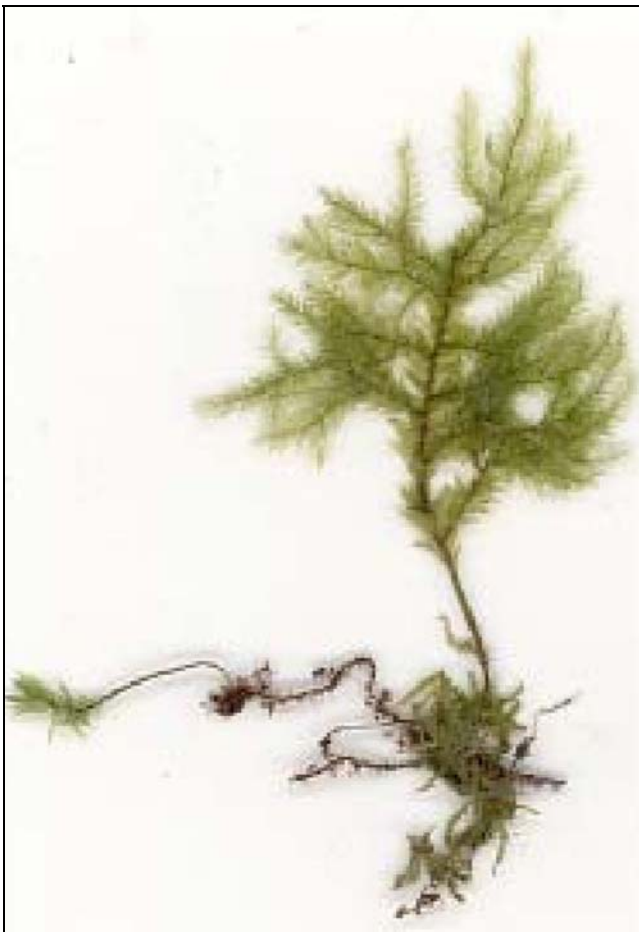


Figure 13. *Porotrichodendron superbum*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 14. *Prionodon densus*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 15. *Neckera cephalonica*; *N. chilensis* occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 16. *Plagiochila adianthoides* from the Neotropics, in a genus that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Here it is showing a **pendent** life form. Photo by Michael Lüth, with permission.

Nadkarni (1984) was among the early Neotropical researchers who investigated ecology of the epiphytes. Unfortunately for us, these typically included the bryophytes, lichens, and tracheophytes together. Nevertheless, we can generally consider that most of the dead epiphyte biomass that accumulates is comprised of bryophytes. On a single large tree (*Clusia alata*), the standing crop was 141.9 kg, with the nutrient concentrations of N 3062 g, P 97 g, K 678 g, ca 460 g, Mg 126 g, and Na 207 g. Despite contributing only 2% to the biomass of the elfin forest dry weight, they contribute approximately 45% of the nutrients. This gives them a considerable role in the nutrient cycling of the cloud forest.

In a later study, Nadkarni *et al.* (2004) distinguished the role of bryophytes. The canopy organic matter in a primary montane cloud forest of Monteverde, Costa Rica, was 63% dead organic matter. Bryophytes comprised 12% of this. However, in the secondary cloud forest, bryophytes provided 95% of the biomass, with only 3% as dead organic matter. Branch junctions in the primary forest supported only dead organic matter and roots, whereas branch tips, subcanopy, and understory substrates supported only bryophytes. Trunks had diverse organic matter components, but little associated dead organic matter. The secondary forest, on the other hand, exhibited little differentiation between trunks and branches due to the dominance of bryophytes. The absence of bryophytes in branch junctions of both forest types is in stark contrast to their common appearance in these location in temperate forests.

Colonization and Life Strategies

A major problem for tropical bryophytes is that those with the common epiphytic life style must get dispersed and then become established on a vertical or otherwise elevated substrate. It is likely to be even more difficult for seeds of larger plants to become so established, so the bryophytes have an important role in providing a catchment for these propagules. Hence, the establishment of the bryophyte biomass is crucial to the cloud forest ecosystem. Nadkarni and coworkers (2000) attempted to determine how successful the bryophytes were in becoming

established from macroscopic fragments onto branches in a tropical cloud forest in Costa Rica (Figure 17). Not surprisingly, only 1% of the bryophyte fragments managed to land and remain on saplings for the six months of study. However, those dropped on the canopy were more successful. Those branches with intact epiphytes retained 24% of the fragments, whereas stripped branches in the same area retained only 5%. This suggests that larger-diameter branches are more successful at retaining the fragments, as are other epiphytes. After 10 years, the bryophytes showed good recovery (Figure 18) (Nadkarni 2000).



Figure 17. Cloud forest fog at Monte Verde, Costa Rica. Photo courtesy of David Fenlon.

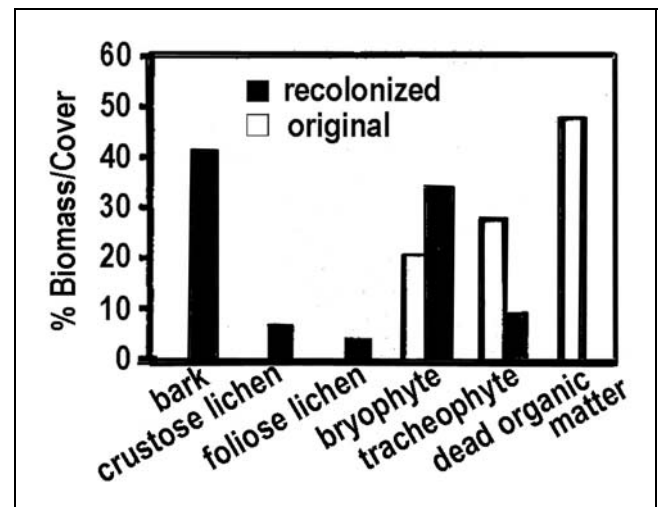


Figure 18. Comparison of component abundance in percent biomass of **original** epiphytic vegetation and percent total cover of **recolonizing** vegetation after 10 years on 75 m segments of inner canopy branches of mature trees at Monteverde, Costa Rica. Redrawn from Nadkarni 2000.

Life forms such as **feather**, **dendroid**, and **large cushions**, and **pendent** forms of *Meteoriaceae* (Figure 72- Figure 73), *Phyllogoniaceae* (Figure 40), *Frullania* (Figure 54), and *Taxilejeunea* (Figure 19) on horizontal branches of small trees and shrubs are often dominant and much more common than in lowland forests (Gradstein & Pócs 1989). Among the cloud forest species is *Fissidens polypodioides* (Figure 20), a member of a very large genus

with more than 500 species (Pursell 1994). In Central America, this is the largest *Fissidens* species, reaching 8 cm. In a Colombian cloud forest (Figure 21), van Leerdam and coworkers (1990) found **tall turfs** and **smooth mats** to predominate in the crowns, with forms differing between the inner and outer canopy. While **smooth mats** are common forms in the higher branches of temperate forests, the **tall turf** would seem to be possible only where moisture is abundant. Surprisingly, they found that growth and life forms differed dependent upon phorophyte species. Epiphyllous forms seem to be limited by frost, occurring up to only about 3,000 m (Pócs 1982).



Figure 19. *Taxilejeunea*, a genus that occurs on horizontal branches of small trees and shrubs in the Neotropics. Photo by Michael Lüth, with permission.



Figure 20. *Fissidens polypodioides*, a cloud forest species that is the largest *Fissidens* species in Central America. Photo by Janice Glime.

The **perennial shuttle species** take advantage of vegetative reproduction to become very important in the epiphytic communities on Mt. Kanabalu, North Borneo, whereas **perennial stayers** take advantage of the spores ultimately resulting from sexual reproduction or the occasional successful fragment to reach a new substrate, where they can persist for a long time (Frey & Kürschner 1991).



Figure 21. Montane cloud forest of Colombia. Photo courtesy of S. Robbert Gradstein.

Species Diversity

The humid cloud forests are important habitats for the leafy liverworts that typically exceed the mosses in number of species. For example, Russell and Miller (1977) found 60 species of epiphytic liverworts, but only 23 of mosses, in an elfin forest in Puerto Rico.

Mandl *et al.* (2010) questioned whether certain species groups could be used as surrogates for diversity in Neotropical montane forests in Ecuador (Figure 22). To test this, they surveyed 28 plots (400 m² each) of both terrestrial and epiphytic species in the ridge and slope forests in three locations in southern Ecuador. The epiphytic habitat had significantly more liverworts than the ground habitat. Mosses, on the other hand, were predominantly ground dwellers. Liverwort diversity proved to be a good indicator of fern α diversity. Moss α diversity was similar to that of ferns and liverworts only in epiphytic habitats. β diversity of ferns, mosses, and liverworts was similar among ground species, but not among epiphytic species. Thus, α diversity is not a good surrogate for β diversity in these cloud forests.



Figure 22. Montane cloud forest in Ecuador. Photo by Nils Köster, courtesy of S. Robbert Gradstein.

In a lower montane cloud forest at Monteverde, Costa Rica, Gradstein *et al.* (2001b) identified 133 liverwort, 56 moss, and 1 hornwort species. The thick branches of the lower canopy were the most species rich, with 99 species,

whereas trunks 1 m and above supported only 65 species. The lianas, shrubs, saplings, and understory leaves had only 36-46 species. Rotten logs were even more limited, with only 16 species. Roughly 36% of the species were exclusively in the canopy, with half the corticolous ones occurring there. In this case, the percentage of bryophyte species restricted to the canopy differs little from that of lowland and montane rainforests.

The Monteverde cloud forest has many rotting logs and fallen branches (Gradstein *et al.* 2001b). These serve as important habitats for the thallose liverworts *Monoclea gottschei* (Figure 23) and *Riccardia* spp. (Figure 24) and the mosses *Trachyxiphium guadalupense* (Figure 25) (Pilotrichaceae), *Mittenothamnium reptans* (Hypnaceae; Figure 26-Figure 27), *Plagiomnium rhynchophorum* (Mniaceae; Figure 28), and *Pyrrobryum spiniforme* (Rhizogoniaceae; Figure 29). Only one hornwort (*Nothoceros vincentianus*; Figure 30) was found in the study, and this could be found on rotten logs. The rotten log species were also frequently encountered on tree bases, especially rotten humus ones.



Figure 23. *Monoclea gottschei*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 24. *Riccardia fucoidea* from the Neotropics; the genus *Riccardia* is a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 25. *Trachyxiphium guadalupense*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 26. *Mittenothamnium reptans*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 27. *Mittenothamnium reptans* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 28. *Plagiommium rhynchophorum*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 29. *Pyrrhobryum spiniforme*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

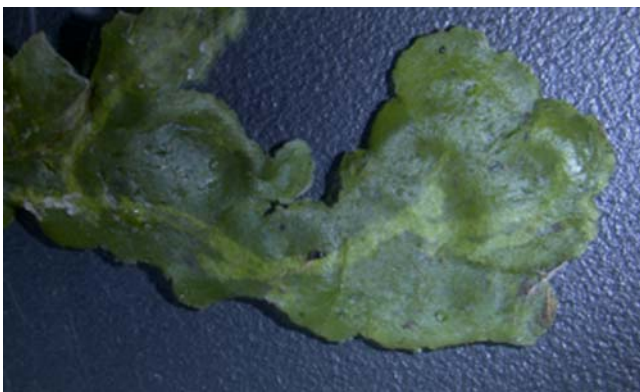


Figure 30. *Nothoceros vincentianus*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. This one is inhabited by a leaf-miner that has made the lighter green paths. Photo courtesy of Juan Carlos Villareal.

Gradstein *et al.* (2001b) elaborated on the species found in the various levels of this Monteverde cloud forest, where they identified 190 species. Unlike some wet forests where *Lejeunea* (Figure 31) presents the most species, in this case that role belonged to *Plagiochila* (Figure 16). In the understory, the most frequent bryophytes on trunks, shrubs, lianas *etc.* were the moss *Porotrichum korthalsianum* (see Figure 32) and the leafy liverworts *Plagiochila* spp. and *Radula antillana* (see Figure 33),

with other common taxa including *Lepidopilum muelleri* (see Figure 34-Figure 35), *Metzgeria leptoneura* (Figure 36), *Omphalanthus filiformis* (Figure 37), *Taxilejeunea pterigonia* (see Figure 38), and *Trichocolea tomentosa* (Figure 39). The well-lit sites were largely characterized by the pendent mosses *Phyllogonium fulgens* (Figure 40) in particular and various *Meteoriaceae* (Figure 54; Figure 72-Figure 73). These often occurred together with the robust liverworts *Porella swartziana* (see Figure 41), *Bryopteris filicina* (Figure 42), *Plagiochila* spp. (Figure 9, Figure 16), and *Radula gottscheana* (see Figure 33).



Figure 31. *Lejeunea flava* on a leaf; *Lejeunea* is common in wet forests, but not in the cloud forests of Monteverde. Photo by Yang Jia-dong, through Creative Commons.



Figure 32. *Porotrichum madagassum*; in a Montverde cloud forest, *Porotrichum korthalsianum* is common on trunks, shrubs, lianas *etc.* Photo by Nicola van Berkel, through Creative Commons.



Figure 33. *Radula* from the Neotropics, a genus that is frequent in the understory on trunks, shrubs, and lianas in the cloud forests of Monteverde. Photo by Michael Lüth, with permission.



Figure 36. *Metzgeria* from the Neotropics; in a Montverde cloud forest, *M. leptoneura* is common on trunks, shrubs, lianas etc. Photo by Michael Lüth, with permission.



Figure 34. *Lepidopilum* from the Neotropics; *Lepidopilum muelleri* is common on trunks, shrubs, lianas etc. in the Montverde cloud forest. Photo by Michael Lüth, with permission.



Figure 37. *Omphalanthus filiformis*, an understory species in the Monteverde cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 35. *Lepidopilum* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 38. *Taxilejeunea* Neotropics; *T. pterigonia* is common on trunks, shrubs, lianas etc. in the Montverde cloud forest. Photo by Michael Lüth, with permission.



Figure 39. *Trichocolea* sp.; *T. tomentosa* is common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by George Shepherd, through Creative Commons.



Figure 40. *Phyllogonium fulgens* from the Neotropics, a species common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by Michael Lüth, with permission.



Figure 41. *Porella obtusata*; *P. swartziana* is a species common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by Kristian Hassel, through Creative Commons.



Figure 42. *Bryopteris filicina*, a species common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by Eliana Calzadilla, through Creative Commons.

Trunk bases at Monteverde (Figure 44) typically had the liverworts *Cephalozia crassifolia* (Figure 43), *Lophocolea connata* (see Figure 45), *Telaranea nematodes* (Figure 46), and various species of *Lejeunea* (Figure 31). Mosses here included *Fissidens* spp. (Figure 20) and *Hypopterygium tamariscinum* (Figure 47) (Gradstein *et al.* 2001b). Less common, but nevertheless characteristic trunk base species, were the leafy liverworts *Calypogeia* spp. and the thallose liverwort *Pallavicinia lyellii* (Figure 48), and the mosses *Cyrt-hypnum schistocalyx* (Figure 49), *Leskeodon andicola* (Figure 50), *Octoblepharum erectifolium* (Figure 51), and *Syrrophodon* spp. (Figure 52). Species of the liverwort *Bazzania* (Figure 53) could also be found, but these are much more common in the forest canopy.

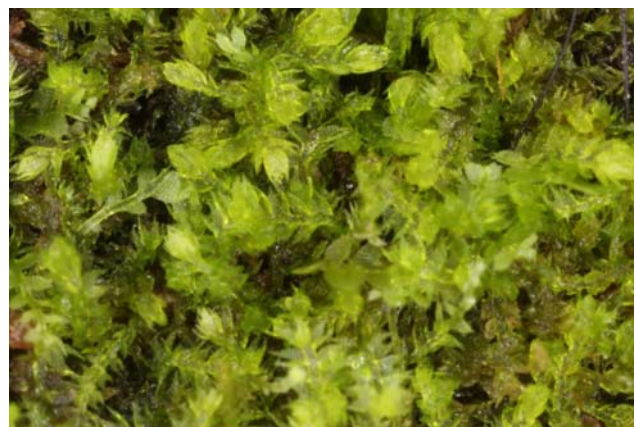


Figure 43. *Cephalozia crassifolia*, a species found on trunk bases at Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

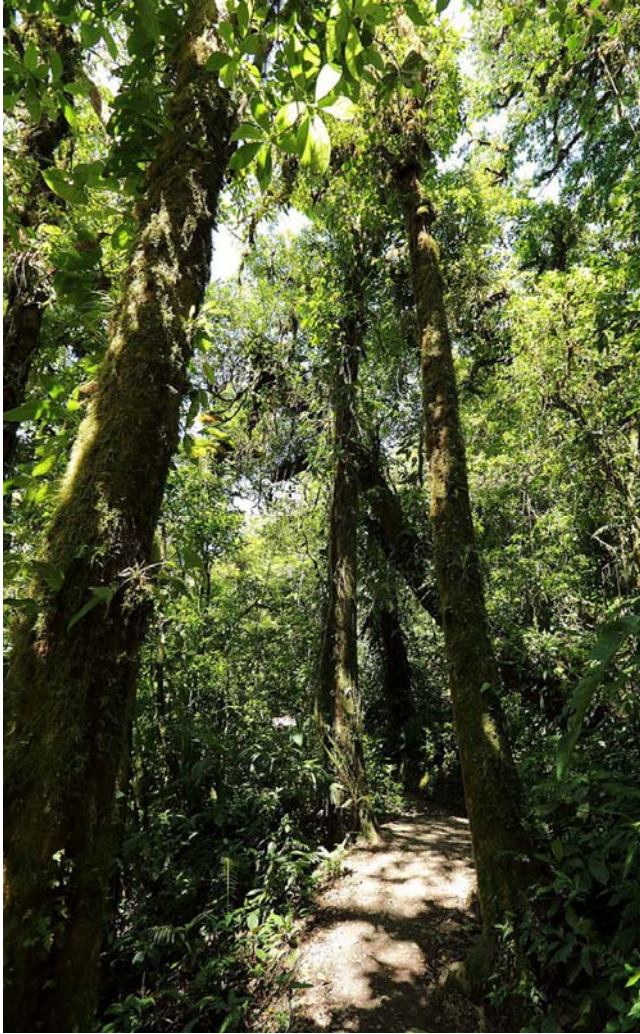


Figure 44. Cloud forest, Monteverde Reserve, Costa Rica. Photo by Cephas, through Creative Commons.



Figure 46. *Telaranea nematodes*, a species found on trunk bases at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 47. *Hypopterygium tamariscinum*, a species found on trunk bases at Monteverde, Costa Rica. Photo by Efrain de Luna, with permission.



Figure 45. *Lophocolea cf polychaeta* from the Neotropics; *L. connata* is a species found on trunk bases at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 48. *Pallavicinia lyellii* with sporophytes, a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 49. *Cyrto-hypnum schistocalyx*, a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 52. *Syrrhopodon gaudichaudii* from the Neotropics; there are several *Syrrhopodon* tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 50. *Leskeodon andicola*, a tree base species in the Monteverde cloud forest, Costa Rica. Photo from Natural History Museum, London, through Creative Commons.



Figure 53. *Bazzania* from the Neotropics; a tree base genus in the Monteverde, Costa Rica, cloud forest. Photo by 3 Michael Lüth, with permission.



Figure 51. *Octoblepharum albidum*; *O. erectifolium* is a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Javier Alejandro, through Creative Commons.

The canopy in the Monteverde cloud forest (Figure 44) demonstrated different communities (Gradstein *et al.* 2001 b). The nearly horizontal branches of the lower canopy displayed these mats of bryophytes. These included the leafy liverworts *Bazzania* (Figure 53), *Frullania convoluta* (Figure 54), *Herbertus* (Figure 55-Figure 56), *Lepidozia* (Figure 57), and *Plagiochila* (Figure 16), and the moss *Macromitrium* (Figure 58). Thick canopy branches added more *Frullania* plus the leafy liverworts *Adelanthus* (Figure 59), *Ceratolejeunea* (Figure 60), *Kurzia capillaris* (Figure 61), *Leptoscyphus porphyrius* (see Figure 62), *Syzygiella pectiniformis* (see Figure 63), and *Acrobolbus latus* (Figure 64).



Figure 54. *Frullania convoluta*, a canopy species in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 55. *Herbertus aduncus* forming deep cushions on branches, a typical sight to be found in the Monteverde, Costa Rica, cloud forest. Botany Website, UBC, with permission.



Figure 56. *Herbertus runcinatus* from Chile. Photo by Blanka Aguero, with permission.



Figure 57. *Lepidozia cupressina* from the Neotropics; *Lepidozia* is a common genus on the horizontal branches in the cloud forest at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 58. *Macromitrium microstomum* on rock; *Macromitrium* is frequent on lower branches in the Monteverde, Costa Rica, cloud forest. Photo by Tom Thekathyl, Blue Tier, with permission.



Figure 59. *Adelanthus decipiens*; the genus *Adelanthus* occurs on thick canopy branches in the cloud forest of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 60. *Ceratolejeunea cubensis*; thick canopy branches support mats of members of *Ceratolejeunea* in the cloud forest of Monteverde, Costa Rica and in the lowland cloud forest in French Guiana. Photo by Scott Zona, through Creative Commons.



Figure 61. *Kurzia capillaris* from the Neotropics, a species that occupies thick branches in the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 62. *Leptoscyphus azoricus*; thick canopy branches support mats of members of *Leptoscyphus* in the cloud forest of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 63. *Syzygiella autumnalis*; thick canopy branches support mats of members of *Syzygiella* in the cloud forest of Monteverde, Costa Rica. Photo by H. Tinguy, French National Museum of Natural History, with online permission.



Figure 64. *Acrobolbus laxus*, a species that occupies thick branches in the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

Mosses of the canopy included *Acroporium pungens* (Figure 65), *Bryum capillare* (Figure 66), *Campylopus arctocarpus* (Figure 67), *Leucobryum giganteum* (Figure 68), *Leucoloma cruegerianum* (Figure 69), *Pilotrichella flexilis* (Figure 11), *Squamidium nigricans* (see Figure 70), and *Syrrhopodon lycopodioides* (Figure 71) (Gradstein *et al.* 2001). Some moss species were generalists: *Toloxis imponderosa* (Figure 72-Figure 73), the pendent *Phyllogonium* (Figure 40), and *Cheilolejeunea filiformis* (see Figure 74), occurring in both the canopy and the understory. The fine twigs in the outer canopy supported communities of the moss *Daltonia gracilis* (see Figure 75) and many small species of the leafy liverwort family *Lejeuneaceae* (Figure 31, Figure 74). And of course the *Lejeuneaceae* predominated on leaves, especially in the understory. These *Lejeuneaceae* included *Cololejeunea* (Figure 76), *Cyclolejeunea convexistipa* (Figure 77), *C. peruviana* (Figure 78), *Drepanolejeunea* (Figure 79), and *Odontolejeunea lunulata* (Figure 80). Overall, 52% of the species are exclusive to the canopy and 20% to the forest understory.



Figure 65. *Acroporium pungens* in the cloud forest of the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.



Figure 66. *Bryum capillare* with capsules, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo from Northern Defences, through Creative Commons.



Figure 67. *Campylopus arctocarpus*, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 68. *Leucobryum giganteum*, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 69. *Leucoloma cf. cruegeriana*, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 70. *Squamidium* from Toro Negro, Puerto Rico; *S. nigricans* occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Janice Glime.

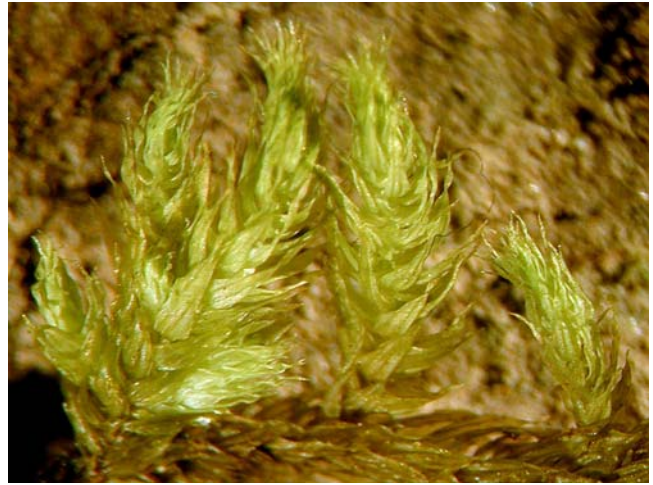


Figure 73. *Toloxis imponderosa* from the Neotropics, where it is a generalist in the canopy. Photo by Michael Lüth, with permission.



Figure 71. *Syrrhopodon lycopodioides* from the Neotropics, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 74. *Cheilolejeunea* from the Neotropics; *Cheilolejeunea filiformis* is a pendent generalist species in the canopy and understory of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 72. *Toloxis imponderosa* from the Neotropics, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 75. *Daltonia cf. longifolia* with capsules; *D. gracilis* occurs on the fine twigs of the outer canopy in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 76. *Cololejeunea cardiocarpa*; the genus *Cololejeunea* occurs on leaves in the Monteverde, Costa Rica, cloud forest. Photo by Paul Davison, with permission.



Figure 77. *Cyclolejeunea convexistipula*; this species occurs on leaves of the understory in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 78. *Cyclolejeunea peruviana*; this species occurs on leaves in the understory of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 79. *Drepanolejeunea mosenii*; the genus *Drepanolejeunea* occurs on leaves, especially in the understory of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 80. *Odontolejeunea lunifolia*; this species occurs on leaves of the understory in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

The epiphytic biomass and the associated canopy humus and canopy water storage capacity vary greatly among old-growth tropical montane cloud forests (Köhler *et al.* 2007). Köhler and coworkers compared the epiphytes in an old-growth cloud forest and a 30-year-old secondary forest on wind-exposed slopes in the Cordillera de Tilarán (Figure 81) in northern Costa Rica where bryophytes were the dominant epiphytes. Epiphyte biomass and canopy humus of the old-growth forest (16,215 kg ha⁻¹) greatly exceeded that of the secondary forest (1,035 kg ha⁻¹). These old-growth forests held water contents of 36%-418% of their dry weights. Stand water storage of the non-tracheophyte epiphytes in the secondary forest was only 0.36 mm, compared to 4.95 mm in the old-growth forest. The bryophytes experienced more dynamic wetting and drying cycles when compared to canopy humus.



Figure 81. Monteverde, Costa Rica, cloud forest, Cordillera de Tilarán. Photo by Peter Andersen, through Creative Commons.

Bubb *et al.* (2004) suggested that bryophytes could serve as indicator species to map the distribution of cloud forests. Because the cloud forest bryophyte species are so sensitive to levels of atmospheric humidity, many have very restricted habitat requirements.

In the Pacific region, many tropical montane cloud forests occur as isolated patches on peaks of volcanoes or rugged upland ridges (Merlin & Juvik 1995). These typically have high rainfall, but also receive "horizontal precipitation" from wind-driven cloud water.

Nadkarni and Solano (2002) expressed concern that climate change models predict reduced cloud water in the tropical montane forests. This could greatly reduce the number of cloud forests in the world. They tested the effects of reduced cloud water on epiphytes by transplanting them, along with their arboreal soil, from the upper cloud forest trees to trees at slightly lower elevation where less cloud water was available. There were no transplantation effects among the controls that remained in the cloud forest. However, those transplanted to the lower elevations had significantly higher leaf mortality, lower leaf production, and reduced longevity. Although these were predominately tracheophytes, it raises the question of survivability of bryophytic epiphytes as well.

Sillett *et al.* (1995) demonstrated a reduction in species when comparing bryophytes in inner tree crowns of *Ficus tuerckheimii* (Figure 82) isolated in a pasture (76 species) with those from an intact cloud forest (109 species) in Costa Rica. Of these, 52 species occurred only on the intact forest trees, whereas only 18 were exclusive to the pasture trees. The intact forest similarly had significantly higher bryophyte species richness, cover, and frequency of **pendants, tall turfs, tails, and fans**. The isolated pasture tree epiphytes experienced higher rates of evaporation and more sunlight compared to those on forest trees. This corresponded with a desiccation gradient from the intact forest to the isolated trees.



Figure 82. *Ficus tuerckheimii*, a species that has more inner crown epiphytes in the forest than when the tree is in the open. Photo by Dick Culbert, with online permission.

Additional studies include those on the microclimate and ecology (Baynton 1968) and ecology of leafy liverworts (Fulford *et al.* 1971a, b) of Puerto Rican cloud forests.

As in so many other studies, Gradstein *et al.* (1977) found "numerous" species of **Lejeuneaceae** (Figure 31, Figure 74), as well as **Plagiochilaceae** (Figure 16). Characteristic species were *Lepicolea pruinosa* (see Figure 83), *Riccardia fucoidea* (Figure 24), and *Scapania portoricensis* (see Figure 84), as well as multiple species of *Bazzania* (Figure 53), *Frullania* (especially **pendulous** species of the section *Meteoriopsis*; Figure 54), *Herbertus* (Figure 55-Figure 56), *Lepidozia* (e.g. *L. wallisiana*; see Figure 57), *Lophocolea* (Figure 45), *Metzgeria* (Figure 36), and *Radula* (Figure 33).



Figure 83. *Lepicolea ochroleuca*; *L. pruinosa* is a characteristic cloud forest species in the tropics. Photo by Jan-Peter Frahm, with permission.



Figure 84. *Scapania ornithopodioides*; *Scapania portoricensis* is a characteristic cloud forest species in the tropics. Photo by Michael Lüth, with permission.

Mount Kenya

Mount Kenya (Figure 85-Figure 86) is the highest mountain in Kenya (5,199 m), exceeded in Africa only by Mount Kilimanjaro (Figure 87). The wettest climate on the mountain is the lower southeastern slopes where the predominating weather system comes from the Indian Ocean (Wikipedia 2018b). This area is dominated by very dense montane forest. The mountain experiences two distinct wet seasons and two distinct dry seasons. Hedberg (1969) described the mountain as having winter every night and summer every day – a challenging climate for most organisms. See also Chamberlin and Okoola (2003) for a discussion of the rainy and dry seasons in eastern Africa.



Figure 85. Mt. Kenya at sunrise. Photo by Alpsdake, through public domain.



Figure 86. Near timberline forest with mosses, Mt. Kenya. Photo by Mehmet Karatay, through Creative Commons.



Figure 87. Mt. Kilimanjaro at Amboseli National Park, Tanzania. Photo by Ninara, through Creative Commons.

The mountain straddles the equator, so in the northern summer the sun shines on the north side of the mountain and in the southern summer it shines on the south side (Wikipedia 2018b). There is only a one-minute difference between the shortest and longest day of the year, a phenomenon that eliminates the possibility of photoperiod as a trigger for life cycle events or preparation for seasonal changes.

The summit of the mountain is alpine, with most of the precipitation occurring as snow (Figure 85). However, frost serves as the primary water source. Between 2,400 m and 3,000 m asl (the lower part of the mountain), moist air rising from Lake Victoria forms clouds over the western forest zone (Clemens *et al.* 1991). Winds carry these clouds to the summit, where they protect the glaciers from melting by screening out direct sun (Hastenrath 1984).

Karlén *et al.* (1999) provide an historic climate perspective based on fluctuations in the glacier on Mount Kenya (Figure 85). Coe (1967) discusses the ecology of the alpine zone of Mt. Kenya. A somewhat recent expedition to Mt. Kenya revealed 10 new taxa, with two being new to all of Africa (Chuah-Petiot & Pócs 2003). These researchers found many protozoa living in the lobules of the leafy liverwort *Colura kilimanjarica* (see Figure 88).



Figure 88. *Colura leratii* from Fiji; *C. kilimanjarica* houses protozoa on Mt. Kilimanjaro in Africa. Photo courtesy of Tamás Pócs.

Lowland Cloud Forest

Following the lead of Gradstein (2006) in French Guiana, Gehrig-Downie *et al.* (2011) defined this new type of cloud forest in northern South America, the lowland cloud forest (Figure 89). This type of forest occurs in river valleys in hilly areas where high air humidity and morning fog occur (Gradstein *et al.* 2010; Gehrig-Downie *et al.* 2011). The area is a rich epiphyte habitat in central French Guiana (Gehrig-Downie *et al.* 2011). This is most likely a result of the much longer periods of high relative humidity after sunrise. These researchers found significantly more epiphytic biomass in the lowland cloud forest (59 g m^{-2}) than in the lowland rainforest that lacked fog (35 g m^{-2}). Furthermore, epiphyte cover in the lowland cloud forest exceeded that of the lowland rainforest in all forest height zones (Figure 90).



Figure 89. Lowland fog in French Guiana. Photo by Delome, through Wikimedia Commons.

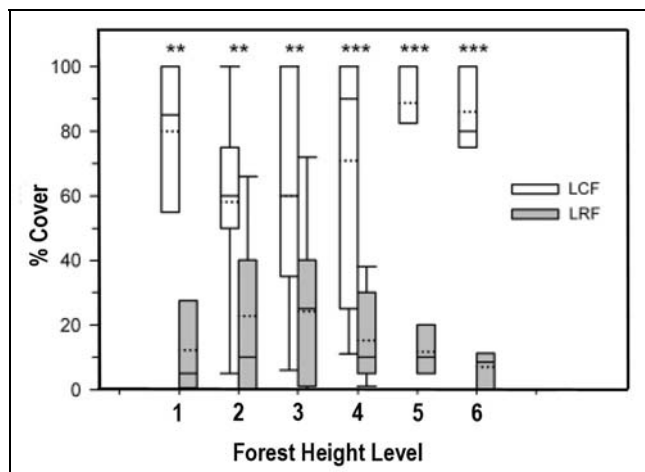


Figure 90. Abundance of all epiphytes as percentage of bark coverage in lowland cloud forest (LCF - white) and lowland rainforest (LRF - grey) in different height zones (1-6) on the tree; N=24 trees per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, dotted line the mean, and whiskers 95th percentile. Levels of significance with unpaired Student t-tests are shown by asterisks, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Modified from Gehrig-Downie *et al.* 2011.

Gradstein (2006) referred to the lowland cloud forest (400 m) of French Guiana (Figure 89) as a "liverwort hotspot." The species richness here is three times that of the Amazonian lowland forest. He found the species

richness of epiphytic liverworts to be similar to that at 2,000 m asl in the Andes. Daytime fog prevents desiccation, permitting a positive net photosynthesis despite the high temperatures. About 30% of the liverwort species are restricted to the canopy and several are obligate epiphylls. Asexual reproduction in the understory is significantly more common than in the canopy. The greater dispersal ability of canopy species, particularly by spores, may explain the greater distributional ranges of species that occur there.

Following up on their earlier studies, Gehrig-Downie *et al.* (2013) described the species differences between lowland cloud forests (Figure 89) and lowland rainforests (Figure 91) in French Guiana. The species composition differs in all height zones, with three times as many indicator species in the lowland cloud forest. The liverwort richness differs more strongly between these two forest types than among the sampled elevations, with lowland cloud forests sometimes being richer in species than even the montane rainforests. Species restricted to the lowland cloud forest and occurring on more than one tree include *Bazzania hookeri* (Figure 92), *Ceratolejeunea coarina* (Figure 93), *Cyclolejeunea chitonia* (see Figure 77-Figure 78), *Metzgeria leptoneura* (see Figure 36), *Pictolejeunea picta*, *Plagiochila cf. gymnocalycina* (see Figure 16, Figure 94), *P. raddiana* (Figure 94), *P. rutilans* (see Figure 16, Figure 94), and *Radula flaccida* (Figure 95). *Ceratolejeunea cubensis* (Figure 60) is the commonest species, occurring in more than 50% of the plots. In the lowland rainforest and collected on more than one tree, the exclusive species are *Anoplolejeunea conferta*, *Diplasiolejeunea cf. cavifolia*, and *D. rudolphiana* (Figure 96). *Cheilolejeunea adnata* (see Figure 74) was present in 80% of lowland rainforest samples, but only in 40% of the lowland cloud forest samples. Liverwort species richness increased with height zone in both forest types. However, in the lowland cloud forest it was the middle and outer crowns where most species occurred, whereas it was highest only in the middle crowns in the lowland rainforest.



Figure 91. French Guiana tropical lowland forest. Photo by Cayambe, through Creative Commons.



Figure 92. *Bazzania hookeri* from the Neotropics, where in French Guiana it is restricted to the lowland rainforests. Photo by Michael Lüth, with permission.



Figure 93. *Ceratolejeunea coarina* perianth, a species that in French Guiana is restricted to the lowland cloud forest. Photo by Michaela Sonnleitner, with permission.



Figure 94. *Plagiochila raddiana* from the Neotropics, where in French Guiana it is restricted to the lowland rainforests. Photo by Michael Lüth, with permission.



Figure 95. *Radula flaccida* habit with gemmae, a species restricted to the lowland cloud forest in French Guiana. Photo by Michaela Sonnleitner, with permission.



Figure 96. *Diplasiolejeunea rudolphiana* from the Neotropics, a species exclusive to the lowland rainforest in French Guiana. Photo by Michael Lüth, with permission.

Cloud forest life forms are benefitted if they are able to take advantage of the moisture in the clouds. Even in lowland rainforests, such as those found in French Guiana, the clouds increase the diversity of epiphytic bryophytes. Compared to other lowland rainforests, the lowland cloud forest exhibits higher biomass and cover of bryophytes, especially in the mid and outer canopy. These bryophytes likewise exhibit a greater diversity of life forms. Typical cloud forest life forms such as **tail**, **weft**, and **pendants** are nearly absent in the canopies of the lowland rainforest, but these are frequent in the lowland cloud forests.

Role

Bryophytes have another important role in these cloud forests. Bruijnzeel and Proctor (1995) emphasized the importance of the tropical montane cloud forest in the water cycle, even in headwater areas. This role is especially important during dry periods, supplying water to downstream areas. Nevertheless, they are often neglected in vegetation studies.

While interception of rainfall in the submontane rainforest is high, that in the elfin forest is about 2.5 times higher and accounts for intercepting over 50% of the annual rainfall (Pócs 1980). The most effective of these receptive bryophytes were the leafy liverworts *Bazzania*

(Figure 92), *Plagiochila* (Figure 94), *Frullania* (Figure 54), *Lepidozia* (Figure 57), and *Trichocolea* (Figure 39). These bryophytes maintain a humid environment beneath by nearly continuous dripping (Lyford 1969 – Puerto Rico; Pócs 1980 – Tanzania) and this seems to create the necessary conditions for terrestrial bryophyte growth. In

montane rainforests of the Colombian Andes, at 3370 m, the epiphyte mass, primarily of bryophytes, was 12 tonnes of dry weight per hectare and held considerable rainfall (Figure 97), which was likewise released very gradually through drainage as well as slow evaporation (Veneklaas *et al.* 1990).

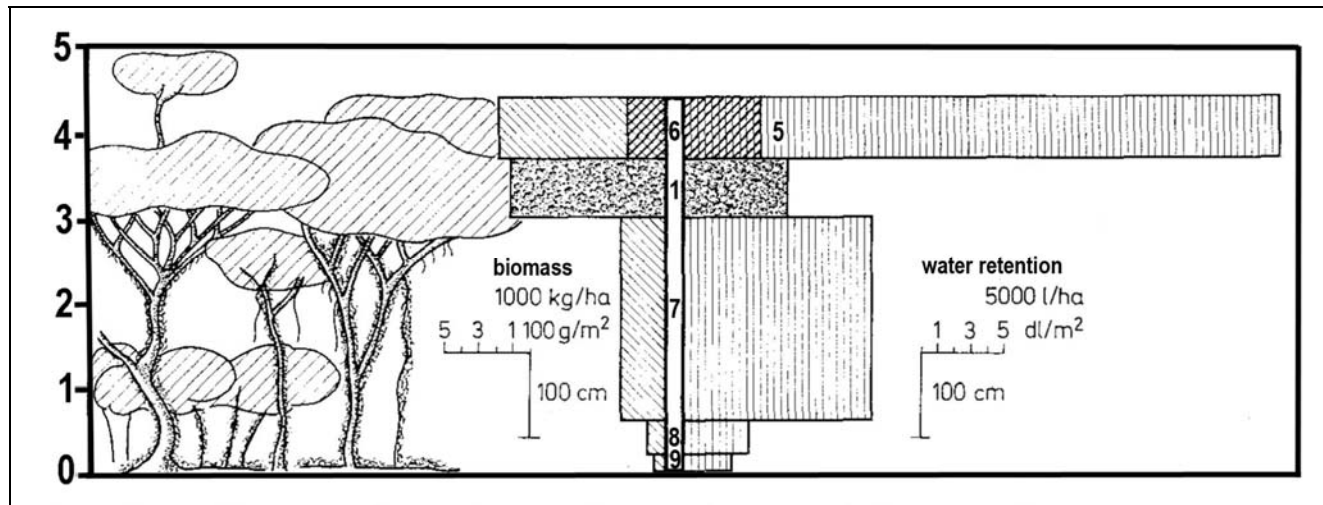


Figure 97. The biomass and interception of water by epiphytes, including bryophytes, and tree leaves in the cloud forest, showing their positions in the forest layers in Tanzania. Modified from Pócs 1980.

Martin *et al.* (2011) remind us that the moisture in a cloud forest reduces fire risk. This same cloud immersion fosters the growth of epiphytic bryophytes (Proctor 1982; Frahm & Gradstein 1991). These bryophytes, in turn, serve as sponges that strip moisture from the air and retain it, further lowering the flammability (Bruijnzeel & Proctor 1995).

Ah-Peng *et al.* (2017) reported excellent cloud water interception ability by the bryophytes in the cloud forest on Reunion Island, using *Bazzania decrescens* (Figure 98) and *Mastigophora diclados* (Figure 99) as study organisms. *Mastigophora diclados* had the greater ability to intercept water, but *Bazzania decrescens* had a far greater water storage capacity. Despite having less than half the abundance of *M. diclados*, *B. decrescens* stored more than twice the water per hectare. The two species combined stored approximately 34,500 L ha⁻¹, the equivalent of 3.46 mm rainfall.



Figure 98. *Bazzania decrescens*, one of the bryophytes that intercepts cloud water in cloud forests on Reunion Island. Photo by Jan-Peter Frahm, with permission.



Figure 99. *Mastigophora diclados*, one of the bryophytes that intercepts cloud water in cloud forests on Reunion Island. Photo by Claudine Ah-Peng, with permission.

In the cloud forests of Papua New Guinea, Norris (1990) found that disturbance could cause serious reduction in the moisture within an epiphytic bryophyte colony. The epiphytes in these tropical cloud forests and rain forests have a much larger biomass than those of temperate forests. He suggested that larger colonies might maintain moisture longer than small colonies. Furthermore, contiguous clones will allow lateral conduction of water, whereas separated tufts result in little if any transfer across the host surface.

That water trapping is not always beneficial to the trees. In places where there are trees, the bryophytes can contribute to their demise. Encircling and hanging from branches, the bryophytes often capture 25% of the precipitation and absorb up to four times their own weight

(Schofield 1985). With this added weight, they can break the branches upon which they rest.

Epiphytes have another interesting role as well in the development of some forest trees. Bryophytes, along with other components (filmy ferns, dead organic matter) of the humus on the branches, provide the moisture and nutrients needed to stimulate adventitious roots, that is, roots that develop from locations other than the base of the stem, in this case from the trunk or branches (Nadkarni 1994b). Using the shrub-tree *Jessea cooperi* (Figure 100), an inhabitant of landslides, she determined that wet epiphytes or nutrient solutions with foam sponges would stimulate the production and growth of adventitious roots, whereas dry epiphytes, distilled water with foam sponges, and dry sponges would not.



Figure 100. *Jessea cooperi*, a species that responds to wet sponges to form adventitious roots, suggesting a possible role for epiphytic bryophytes. Photo by Dick Culbert, through Creative Commons.

As with epiphytes in general, the epiphytes in the cloud forest can provide substrate, water reserves, and nutrient release that are available to tracheophytes. Orchids frequently become established in these mats (Frei 1973).

As with any thick bryophyte mat, the tropical bryophyte assemblages are home for numerous invertebrates. In the cloud forest of Costa Rica, these are likely to include amphipods, isopods, mites, Collembola, larvae, adult beetles, and ants (Nadkarni & Longino 1990). Interestingly, Nadkarni and Longino found that the composition of the fauna was basically the same in the canopy as that on the forest floor, but the ground had a mean density that was 2.6 times as great as that in the canopy, with the exception of ants, which were similar in both.

Subalpine

The sub-alpine (Figure 101) can act like an island, presenting a temperature regime that is more like the Arctic than the tropics. This makes mountaintop extinctions and a

loss of biodiversity a danger under the influence of global climate change (Ah-Peng *et al.* 2014). On Réunion Island, Ah-Peng and coworkers found a relatively high species richness for bryophytes in the subalpine habitats, with diversity peaking at 2750 m asl for the ground-dwellers. They found that the functional richness with elevation differed between ground-dwellers and epiphytes, suggesting differences in the processes that structure these two community types. The ground-dwellers have a higher functional redundancy; the researchers interpreted this to indicate that the ground-dwellers may be more robust than the epiphytes when disturbances occur in this subalpine system.



Figure 101. Tropical subalpine dwarf forest in Peru at 3,200 m asl with Jan-Peter Frahm among the epiphytes. Photo courtesy of S. Robbert Gradstein.

Alpine

Luteyn *et al.* (1999, p. 1; see also Smith & Young 1987) list the different local names applied to the band of vegetation between the upper limit of continuous, closed-canopy forest (**timberline**; Figure 102) and the upper limit of plant life (**snowline**; Figure 103). In tropical regions of Mexico, Central and South America, Africa, Malesia including New Guinea, and Hawaii, this zone typically has tussock grasses, large rosette plants, evergreen shrubs, and cushion plants. These areas have different local names, including *zacatonales* (Mexico, Guatemala; Figure 104), *páramo* (Central and northern South America; Figure 105), *jalca* (northern Peru; Figure 115), *puna* (drier areas of the

altiplane of central Andes; Figure 106), *Afro-alpine* or *moorland* (East Africa; Figure 107), and *tropical-alpine* (Malesia; Figure 108-Figure 109).



Figure 102. **Treeline** (timberline) in Tararua, North Island of New Zealand. Photo by William Demchick, through Creative Commons.



Figure 103. Snowline on Chimborazo volcano, Ecuadorian Andes. Photo by Bernard Gagnon, through Creative Commons.



Figure 104. Zacotal, Nevado de Toluca, Mexico. Photo by Mainau, through public domain.



Figure 105. Páramo in Colombia. Photo by Friedrich Kircher, through Creative Commons.



Figure 106. Central Andean wet puna. Photo by Idobi, through Creative Commons.



Figure 107. Afro-alpine, at Lascar, northern Chile. Photo by Jorge Láscas, through Creative Commons.



Figure 108. Mount Kinabalu, Malaysia, showing tropical alpine region in the distance. Photo by Nep Grower, through Creative Commons.



Figure 109. Mount Kinabalu summit plateau (Afro-alpine). Photo by Ariel Steiner, through Creative Commons.

Bader *et al.* (2007) examined the role of bryophytes in tree regeneration above treeline in Ecuador (Figure 110). It is difficult for tree seedlings to become established there, and the researchers hypothesized that bryophytes could facilitate that establishment. First, they found that the number of naturally occurring tree sprouts (seedlings, saplings, and ramets) was highest just outside the forest, and decreased with distance to the forest edge. They transplanted seedlings into the alpine vegetation. The forest floor is totally covered with mosses, including species of *Sphagnum* (Figure 111), especially at the forest edge, and has a peaty organic layer of 30-100 cm on top of the dark mineral soil. The transplanted seedlings had negligible growth after 2.5 years, and some decreased in size due to damage of upper parts. Others seemed to be shorter due to the growth of fast-growing forest floor mosses that served as the measurement base. The seedlings that were planted in the mosses were sometimes overgrown by the mosses. The researchers concluded that seedlings can grow among mosses in the forest where that is the only available substrate, but that they are not favored by mosses.



Figure 110. *Blechnum loxense* tree fern at treeline in the Ecuadorian Andes at 3,500 m asl, showing tropical researcher Jan-Peter Frahm. Photo courtesy of S. Robbert Gradstein.



Figure 111. *Sphagnum magellanicum*; the genus *Sphagnum* occurs on the forest floor near treeline in Ecuador. Photo by Michael Lüth, with permission.

In the Neotropics, Gradstein *et al.* (2001a) recognized páramo, Puna, and Zacatonal as the alpine habitats. Smith and Young (1987) noted how few studies existed on tropical alpine bryophytes and emphasized their importance in tropical mountain communities.

Páramo

The **páramo** (sparsely vegetated alpine zone on tops of high mountains of Andes and other high-elevation South American mountains; Figure 112-Figure 114) is generally considered to occur in Venezuela, Colombia, and northern Ecuador, with a pocket in Costa Rica (Luteyn 1999; Daniel Stanton, pers. comm. 4 December 2011). In northern Peru, wetter grasslands are known as **jalcas** (Figure 115). As pointed out by Daniel Stanton (pers. comm. 4 December 2011), the differences in naming may be more political or cultural than a reflection of real differences.



Figure 112. Páramo Sumapaz, Colombia. Photo by Yuri Romero Picon, through public domain.



Figure 113. Páramo in Colombia. Photo by Friedrich Kircher, through Creative Commons.



Figure 114. Páramo of Rabanal, Colombia. Photo by Patricio Mena Vásquez, through public domain.



Figure 115. **Jalca** district, Chachapoyas, Peruvian Amazon Region. Photo by Pitxiquini, through Creative Commons.

There is a striking shift in the substrate of bryophytes as one goes up in elevation in many parts of the tropics. Lower elevations, ranging up through the condensation zone and only slightly into the **páramo**, one can find most of the bryophyte cover as epiphytes on trees and shrubs. However, beginning at in the lower montane and increasing dramatically in the páramo, the major bryophytic cover is found on soil and rock for both mosses and liverworts (van Reenen & Gradstein 1983).

Central America enjoys the interesting flora that is a product of influence from both North and South America. In the Cordillera de Talamanca of Costa Rica, Holz (2003) and Holz and Gradstein (2005) identified 191 liverworts, 209 mosses, and 1 hornwort. Of these, 128 liverworts, 122 mosses, and 1 hornwort occur in the oak (*Quercus*) forests. The bryophytes are represented by proportionally more tropical species than are the tracheophytes. In the páramo, by contrast, the bryophyte flora is more similar to that of temperate regions. There are fewer endemics than are found in the oak forests.

Table 1. Ten largest families and genera of páramo mosses and liverworts. From Holz & Gradstein 2005.

Family (no. genera/spp.)	Genus (family) (no. spp.)
Mosses (prepared by Steve Churchill and Dana Griffin III)	
Dicranaceae (17/67) – Figure 3	Sphagnum (Sphagnaceae) (37) – Figure 111
Bryaceae (10/65) – Figure 121, Figure 123	Zygodon (Orthotrichaceae) (21) – Figure 116
Pottiaceae (19/63) – Figure 159	Bryum (Bryaceae) (18) – Figure 121
Bartramiaceae (7/40) – Figure 120	Leptodontium (Pottiaceae) (16) – Figure 140
Orthotrichaceae (3/36) – Figure 116, Figure 117	Orthotrichum (Orthotrichaceae) (14) – Figure 117
Sphagnaceae (1/27) – Figure 111	Breutelia (Bartramiaceae) (13) – Figure 120
Amblystegiaceae (9/19) – Figure 118-Figure 119	Daltonia (Daltoniaceae) (13) – Figure 122
Brachytheciaceae (7/18) – Figure 141	Macromitrium (Macromitriaceae/Orthotrichaceae) – Figure 58
Polytrichaceae (6/16) – Figure 158	Schizymenium (Bryaceae) (11) – Figure 123
Grimmiaceae (4/17) – Figure 132-Figure 133	
Liverworts (prepared by Robbert Gradstein)	
Lejeuneaceae (16/38) – (Figure 31, Figure 74)	Riccardia (Aneuraceae) (20) – (Figure 24)
Jungermanniaceae (11/31) – Figure 149	Metzgeria (Metzgeriaceae) (20) – Figure 124
Lepidoziaceae (6/20) – Figure 57	Plagiochila (Plagiochilaceae) (18) – Figure 16, Figure 94
Aneuraceae (2/21) – (Figure 24)	Frullania (Jubulaceae/Frullaniaceae) (13) – Figure 54
Metzgeriaceae (1/20) – Figure 124	Bazzania (Lepidoziaceae) (13) – Figure 98
Plagiochilaceae (2/19) – Figure 16, Figure 94	Anastrophyllum (Jungermanniaceae/Anastrophyllaceae) (8) – Figure 149
Geocalycaceae (7/18) – Figure 62	Lepidozia (Lepidoziaceae) (8) – Figure 57
Gymnomitriaceae (5/14) – Figure 129-Figure 130	Leptoscyphus (Geocalycaceae) (7) – Figure 62
Jubulaceae/Frullaniaceae (1/13) – Figure 54	Isotachis (Balantiopsidaceae) (6) – Figure 125
Balantiopsaceae (2/7) – Figure 125	Cephaloziella (Cephaloziellaceae) (6) – Figure 126
	Marsupella (Gymnomitriaceae) (6) – Figure 129-Figure 130
	Radula (Radulaceae) (6) – Figure 33



Figure 116. *Zygodon conoideus*, with capsules, representing one of the 10 largest families in the páramo. Photo by Proyecto Musgo through Creative Commons.



Figure 117. *Orthotrichum rupestre* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 118. *Vittia pachyloma* habitat in Chile, representing one of the 10 largest families in the páramo. Photo by Juan Larrain, with permission.



Figure 121. *Bryum apiculatum* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 119. *Vittia pachyloma*, representing one of the 10 largest families in the páramo. Photo from NYBG, through public domain.



Figure 122. *Daltonia cf. longifolia* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 120. *Breutelia wainioi* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 123. *Schizymenium pontevedrense* with capsules, in a genus that is common in the páramo in the Neotropics. Photo by Michael Lüth, with permission.



Figure 124. *Metzgeria* in the Neotropics, representing one of the 10 largest families (**Metzgeriaceae**) in the páramo. Photo by Michael Lüth, with permission.



Figure 125. *Isotachis aubertii* in the Neotropics, representing one of the 10 largest families (**Balantiopsidaceae**) in the páramo. Photo by Michael Lüth, with permission.



Figure 126. *Cephaloziella exiliflora*, in a genus that is common in the páramo of the Neotropics. Photo by Tom Thekathyl, with permission.

One reason for the low number of bryophyte taxa at lower elevations might be due to nighttime respiratory losses. High nighttime temperatures in the lowlands elevate the loss of CO₂ and prevent the bryophytes from attaining a net positive carbon balance (Proctor 1982; Richards 1984; Frahm 1987, 1990, 1994; Zotz *et al.* 1997; Zotz 1999). This is consistent with observations that the distribution correlates with increased moisture and lower temperatures at higher elevations (Pôrto 1992), permitting more time per day for photosynthetic gain.

Other studies on the páramo include liverwort diversity in the Neotropics (Gradstein 1998) and bryophytes and lichens of the páramo (Griffin 1979). Cleef (1978) described the Neotropical páramo vegetation and its relationship to that of the subAntarctic. Mägdefrau (1983) described bryophyte vegetation in the páramo of Venezuela and Colombia.

Moss Balls

Moss balls, also known as **vagrant plants**, erratic, solifluction floaters, and errant cryptogams (Pérez 1997b), are unattached plants that are blown about by the wind or moved by water or frost-heaving. Because of their movement, they frequently change their upward direction and consequently begin growth in a different direction (Shacklette 1966). This, and the tumbling that can break off extruding parts, forms them into balls. These are somewhat common on bare soils where climate conditions are subarctic, creating lenticular to spherical moss balls that are completely unattached and free to blow about on the snow and ice (Beck *et al.* 1986). These moss balls are particularly abundant in the alpine zone of high mountains of tropical Africa, especially on Mt. Kenya. In that location, the balls are formed by *Grimmia ovalis* (Figure 127-Figure 128). These are formed by continual motion of fragments of cushions that have been broken by frost or by single plants or small aggregations that occur on bare soil. These vulnerable bryophytes can be moved by wind and solifluction that occurs due to nocturnal needle-ice formation and subsequent thawing in the daytime. The outer layer of the balls that are formed is the living part; next is a layer of dead plant sections, whereas the core is a peaty material of disintegrated leaflets, rhizoids, stems, and minute soil particles.



Figure 127. *Grimmia ovalis*, a species that is able to form moss balls. Photo by Michael Lüth, with permission.



Figure 128. *Grimmia ovalis* forming balls that can break away to form moss balls. Photo by Barry Stewart, with permission.

Others, in particular *Marsupella* (Figure 129-Figure 130), occur on small soil buds and nubbins that are common on the ground surface in the high páramo (Pérez 1994). The moss balls are known in many biomes where wind or water create them. In the superpáramo zone, frost-heaving creates such moss balls, as also seen in the fruticose lichen *Thamnolia vermicularis* (Figure 131) and the acrocarpous moss *Grimmia longirostris* (Figure 132) (Pérez 1991, 1994). Members of *Grimmiaceae* seem to be suited to making vagrant populations. Shacklette (1966) reported unattached polsters (known as glacier moss) of *Schistidium apocarpum* (Figure 133) on sandy soil on Amchitka Island, Alaska, where they become detached by wind erosion.



Figure 129. *Marsupella emarginata* var. *pearsonii*; *Marsupella* occurs on small soil buds and nubbins that are common on the ground surface in the high páramo. Photo by Michael Lüth, with permission.



Figure 130. *Marsupella emarginata*, a species that can form bryophyte balls. Photo by Michael Lüth, with permission.



Figure 131. *Thamnolia vermicularis*, a species that forms balls in the superpáramo. Photo by Schaudé, through Creative Commons.



Figure 132. *Grimmia longirostris* moss balls created by solifluction. Photo by Henk Greven, with permission.



Figure 133. Glacier mice – moss balls, probably *Schistidium apocarpum*. Photo from Wondergressive, through Creative Commons.

Afro-alpine

In most people's minds, the combination of African and alpine (Figure 134) seems like an oxymoron. Nevertheless, Afro-alpine zones exist and present unique communities (Hedberg 1964). The *Dendrosenecio* (Figure 135) woodlands present *Breutelia diffracta* (Figure 136), *B. stuhlmannii* (Figure 137), *Brachythecium ramicola*, *Campylopus nivalis* (Figure 138), *Sanionia uncinata* (Figure 139), and *Leptodontium viticulosoides* (Figure 140). The bottom layer is characterized by the mosses *Brachythecium ruderales* (Figure 141), *B. spectabile*, and *Hypnum bizotii*, and the liverworts *Chiloscyphus cuspidatus* (Figure 142), *Lophocolea martiana* (see Figure 45), *Metzgeria hamata* (Figure 143), *M. hedbergii*, *Mylia hedbergii* (see Figure 144), and *Plagiochila haumanii* (see Figure 16, Figure 94).



Figure 134. Mt. Kenya. Photo by Elizabeth Kiragu Wanjugu and Tobias Schonwetter, through Creative Commons.



Figure 135. *Dendrosenecio*, a tree found in the Afroalpine zone. Photo through Creative Commons.



Figure 136. *Breutelia diffracta*, a species in the *Dendrosenecio* woodlands of the Afroalpine region. Photo by Jan-Peter Frahm, with permission.



Figure 137. *Breutelia stuhlmannii*, a species in the *Dendrosenecio* woodlands of the Afroalpine region. Photo by Jan-Peter Frahm, with permission.



Figure 138. *Campylopus nivalis*, a species in the *Dendrosenecio* woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.



Figure 141. *Brachythecium ruderales*, a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by Claudio Delgadillo Moya, with permission.



Figure 139. *Sanionia uncinata*, a species in the *Dendrosenecio* woodlands of the Afromontane region. Photo by Michael Lüth, with permission.



Figure 142. *Chiloscyphus cuspidatus*, a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo from the TePapa collection, through Creative Commons.



Figure 140. *Leptodontium viticulosoides*, a species of *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by Li Zhang, with permission.



Figure 143. *Metzgeria hamata*, a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 144. *Mylia anomala*; *M. hedbergii* is a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by David T. Holyoak, with permission.

Older stems of the *Dendrosenecio* (Figure 135) commonly support thick cushions of moss, with lichens being relatively rare (Hedberg 1964). These include numerous bryophyte species, but the moss *Antitrichia curtispindula* (Figure 145-Figure 146) is the most abundant.

Accompanying species include the moss *Hypnum cupressiforme* (Figure 147-Figure 148) and the leafy liverworts *Anastrophyllum auritum* (see Figure 149), *Lophocolea mollerii* (see Figure 150), *Plagiochila colorans* (Figure 16, Figure 94), and *Radula boryana* (see Figure 151) (Hedberg 1964). These moss mats support several tracheophytes, including *Polypodium moniliforme* var. *rigescens* (see Figure 152), *Poa schimperiana* (see Figure 153), *Cardamine obliqua* (see Figure 154), *Arabis pterosperma* (Figure 155), and juvenile *Senecio* sp. The ground layer has a nearly continuous carpet of mosses that also cover boulders and decaying stems of *Senecio*/*Dendrosenecio* and *Lobelia* (Figure 156). The important bryophytes in these carpets include the mosses *Brachythecium spectabile* (see Figure 141), *Breutelia diffracta* (Figure 136), *Hylocomium splendens* (common in boreal forests; Figure 157), *Pogonatum urnigerum* (Figure 158), *Syntrichia cavallii* (see Figure 159), and the liverwort *Metzgeria hamata* (Figure 143). Stones typically had a thin cover of *Homalothecium sericeum* (Figure 160). Many additional species were identified on the *Dendrosenecio*. The dominant *Sphagnum* species in the sedge (*Carex*) peatland was *S. strictum* subsp. *pappeanum* (Figure 161), with additional species on and among the grass tussocks.



Figure 145. *Antitrichia curtispindula* habitat. This species is the most abundant on *Dendrosenecio* in the Afromontane. Photo by James K. Lindsey, with permission.



Figure 146. *Antitrichia curtispindula*, the most abundant species on *Dendrosenecio* in the Afromontane. Photo by James K. Lindsey, with permission.



Figure 147. *Hypnum cupressiforme*, a worldwide species that occurs on *Dendrosenecio* in the Afromontane. Photo by Michael Lüth, with permission.



Figure 148. *Hypnum cupressiforme*, a species that occurs on *Dendrosenecio* in the Afromontane. Photo by Michael Lüth, with permission.



Figure 149. *Anastrophillum donnianum*; *Anastrophillum auritum* occurs on *Dendrosenecio* in the Afromontane. Photo by Michael Lüth, with permission.



Figure 150. *Lophocolea semiteres*; *Lophocolea molleri* occurs on *Dendrosenecio* in the Afromontane. Photo by David T. Holyoak, with permission.



Figure 151. *Radula bolanderi*; *R. boryana* occurs on *Dendrosenecio* in the Afromontane. Photo by Ken-ichi Ueda through Creative Commons.



Figure 152. *Polypodium glycyrrhiza* growing among mosses; *P. moniliforme* var. *rigescens* grows among mosses on *Dendrosenecio*. Photo by J. Brew, through Creative Commons.



Figure 153. *Poa annua*; *P. schimperiana* is supported by moss mats on older stems of *Dendrosenecio*. Photo by Rasbak, through Creative Commons.



Figure 155. *Arabis pterosperma*, a species that grows in moss mats on *Dendrosenecio* in the Afromontane. Photo by B. R. Kailash, through Creative Commons.



Figure 154. *Cardamine* sp.; *Cardamine obliqua* grows in moss mats on *Dendrosenecio* in the Afromontane. Photo through Creative Commons.



Figure 156. Giant lobelia (*Lobelia deckenii*) on Mt. Kenya; juvenile lobelias can establish in moss mats. Photo by Mehmet Karatay, through Creative Commons.



Figure 157. *Hylocomium splendens*, a common boreal forest species that occurs in the Afro-montane zone. Photo by Michael Lüth, with permission.



Figure 160. *Homalothecium sericeum*, a species that forms a thin layer on rocks in the Afro-alpine zones. Photo Kristian Peters, through Creative Commons.



Figure 158. *Pogonatum urnigerum*, a species that forms carpets on the forest floor in the Afro-alpine zones. Photo by Michael Lüth, with permission.



Figure 161. *Sphagnum strictum*; *S. strictum* subsp. *pappeanum* is the dominant *Sphagnum* species in the Afro-montane *Carex* peatlands. Photo by Blanka Aguero, with permission.



Figure 159. *Syntrichia ruralis*; *S. cavallii* forms carpets on the forest floor in the Afro-alpine zones. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University with permission from Russ & Karen Blisard.

Summary

The cloud forests have dwarfed trees that are typically covered with bryophytes. Seasonal variation in rainfall in cloud forests can be low or high. **Pendent** bryophytes and **fans** effectively trap water droplets and expose maximum surface area to the light; bryophytes can intercept over 50% of the annual rainfall in cloud forests. Water conservation within the bryophytes is facilitated by elastic cell walls. **Fan** species have low light saturation and low compensation points. Because of the high moisture requirements, the bryophyte species are often restricted to these cloud forests.

Liverworts typically outnumber mosses, but mosses can contribute 54-99% of the biomass. Whereas this biomass is relatively low compared to woody biomass, the bryophytes can contribute 45% of the nutrients through nitrogen fixation and entrapment of nutrients from the air, fog, and precipitation.

Dispersal may occur by fragments, and these are more successful when landing among epiphytes. **Tall turfs** and **smooth mats** predominate in crowns. **Meteoriaceae**, **Phyllogoniaceae**, **Frullania**, and **Taxilejeunea** are the most common taxa on horizontal branches of small trees and shrubs. These are among the typically **perennial shuttles** and **perennial stayers** that dominate the life strategies. Mosses predominate on the ground, liverworts as epiphytes. Instead of the typical **Lejeunea**, **Plagiochila** predominates among the epiphytes at Monteverde, Costa Rica. Nevertheless, the **Lejeuneaceae** is common. Thallose liverworts are common on logs.

Lowland cloud forests are a recent discovery and have a similar high humidity to mountain cloud forests and a species richness often exceeding them. Life forms such as **tail**, **weft**, and **pendants** are nearly absent in the canopies of the lowland rainforest, but these are frequent in the lowland cloud forests. Bryophytes play a major role in the water cycle, with **Bazzania**, **Plagiochila**, **Frullania**, **Lepidozia**, and **Trichocolea** maintaining a humid environment beneath by nearly continuous dripping.

The canopy bryophytes serve to trap dust and contained nutrients, hold moisture, and in some cases provide rooting media. Their cushions hold massive amounts of water, thus maintaining a humid environment long after rainfall ceases. This minimizes fire danger. Unfortunately, their weight sometimes causes the branches to break. The bryophytes also provide habitat for a number of invertebrates.

The subalpine and alpine areas can act as islands because most of their species cannot grow at lower elevations. As one goes up into the alpine region, bryophytes are increasingly found on the soil and rocks. Glaciers and windy alpine tundra provide conditions that create moss balls that blow about on the substrate. Other moss balls are created by and carried by **solifluction** – movement by water. Members of **Grimmiaceae** are particularly common among these moss balls.

Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about.

Literature Cited

- Ah-Peng, C., Flores, O., Wilding, N., Bardat, J., Marline, L., Hedderson, T. A., and Strasberg, D. 2014. Functional diversity of subalpine bryophyte communities in an oceanic island (La Réunion). *Arct. Antarct. Alp. Res.* 46: 841-851.
- Ah-Peng, C., Cardoso, A. W., Flores, O., West, A., Wilding, N., Strasberg, D., and Hedderson, T. A. 2017. The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *J. Hydrol.* 548: 665-673.
- Ash, J. 1987. Stunted cloud-forest in Taveuni, Fiji. *Pacific Sci.* 41: 191-199.
- Bader, M. Y., Geloof, I. van, Rietkerk, M. 2007. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecol.* 191: 33-45.
- Baynton, H. W. 1968. The ecology of an elfin forest in Puerto Rico, 2. The microclimate of Pico del Oeste. *J. Arnold Arbor.* 49: 419-430.
- Beck, E., Mägdefrau, E., and Senser, M. 1986. Globular mosses. *Flora* 178: 73-83.
- Bohlman, S. A., Matelson, T. J., and Nadkarni, N. M. 1995. Moisture and temperature patterns of canopy humus and forest floor soils of a montane cloud forest, Costa Rica. *Biotropica* 27: 13-19.
- Bruijnzel, L. A. and Proctor, J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? In: Hamilton, L. S., Juvik, J. O., and Scatena, F. N. (eds.). *Tropical Montane Cloud Forests*, Ecological Studies vol. 110, Springer-Verlag, New York, N. Y., pp. 38-78.
- Bubb, P., May, I. A., Miles, L., and Sayer, J. 2004. Cloud forest agenda. UNEP-WCMC, Cambridge, UK. A Banson production Printed in the UK by Swaingrove Imaging. <http://www.unep-wcmc.org/resources/publications/UNEP_WCMC_bio_series/20.htm>.
- Camberlin, P. and Okoola, R. E. 2003. The onset and cessation of the "long rains" in eastern Africa and their interannual variability. *Theor. Appl. Climatol.* 75: 43-54.
- Chuah-Petiot, M. S. and Pócs, T. 2003. East African bryophytes XIX. A contribution to the bryoflora of Kenya. *Acta Bot. Hung.* 45: 53-64.
- Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). 1995. *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, N. Y.
- Cleef, A. M. 1978. Characteristics of Neotropical paramo vegetation and its subAntarctic relations. In: Troll, C. and Lauer, W. (eds.). *Geocological relations between the southern temperate zone and the tropical mountains*. *Erdivissenschaftlicher Forschung (Wiesbaden)* 11: 365-390 + 6 t.
- Clemens, S., Prell, W., Murray, D., Shimmield, G., and Graham Weedon, G. 1991. Forcing mechanisms of the Indian Ocean monsoon. *Nature* 353: 720-725.
- Coe, M. J. 1967. The ecology of the alpine zone of Mount Kenya. Dr. W. Junk, Den Haag, Netherlands.
- Dunne, H. J. F. van and Kappelle, M. 1998. Biomass diversity relations of epiphytic bryophytes on small *Quercus copeyensis* stems in a Costa Rican montane cloud forest. *Revis. Biol. Trop.* 46: 217-224.
- Frahm, J.-P. 1987. Which factors control the growth of epiphytic bryophytes in tropical rainforests? *Symp. Biol. Hung.* 35: 639-648.
- Frahm, J.-P. 1990. The effect of light and temperature on the growth of the bryophytes of tropical rain forests. *Nova Hedw.* 51: 151-164.
- Frahm, J.-P. 1994. Scientific results of the BRYOTROP expedition to Zaire and Rwanda 1. The ecology of epiphytic bryophytes on Mt. Kahuzi (Zaire). *Trop. Bryol.* 9: 137-152.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Frei, S. J. K. 1973. Orchid ecology in a cloud forest in the mountains of Oaxaca, Mexico. *Amer. Orchid Soc. Bull.* 42: 307-314.
- Frey, W. and Kürschner, H. 1991. Lebensstrategien epiphytischer Bryophyten im tropischen Tieflands- und

- Bergregenwald am Mt. Kinabalu (Sabah, Nord-Borneo). *Nova Hedw.* 53: 307-330.
- Fulford, M., Crandall, B., and Stotler, R. 1970. The ecology of an elfin forest in Puerto Rico. 11. The leafy Hepaticae of Pico del Oeste. *J. Arnold Arbor.* 51: 56-69.
- Fulford, M., Crandall, B., and Stotler, R. 1971a. The ecology of an elfin forest in Puerto Rico. Part 11. The leafy Hepaticae of Pico del Oeste. *J. Arnold Arbor.* 51: 56-59.
- Fulford, M., Crandall, B., and Stotler, R. 1971b. The ecology of an elfin forest in Puerto Rico. Part 15. A study of the leafy hepatic flora of the Luquillo Mountains. *J. Arnold Arbor.* 52: 435-458.
- Gehrig-Downie, C., Obregón, A., Bendix, J., and Gradstein, S. R. 2011. Epiphyte biomass and canopy microclimate in the tropical lowland cloud forest of French Guiana. *Biotropica* 43: 591-596.
- Gehrig-Downie C., Obregón A., Bendix J., and Gradstein S. R. 2013. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. *J. Bryol.* 35: 243-254.
- Gorchov, D. L., and Cornejo, F. 1993. Forest regeneration after strip-cutting in the Peruvian Amazon: Regeneration mode, survival, and edge effects. *Bull. Ecol. Soc. Amer. Program and Abstracts, Suppl. vol 74(2):* 253. 78th Ann. ESA Meeting, 31 July - 4 August 1993.
- Gotsch, S. G., Nadkarni, N., and Amici, A. 2016. The functional roles of epiphytes and arboreal soils in tropical montane cloud forests. *J. Trop. Ecol.* 32: 455-468.
- Gotsch, S. G., Davidson, K., Murray, J. G., Duarte, V. J., and Draguljić, D. 2017. Vapor pressure deficit predicts epiphyte abundance across an elevational gradient in a tropical montane region. *Botany* 104: 1790-1801.
- Gradstein, S. R. 1998. Hepatic diversity in the Neotropical páramos. *Monogr. Syst. Bot. (Missouri Botanical Garden)* 68: 69-85.
- Gradstein, S. R. 2006. The lowland cloud forest of French Guiana: A liverwort hotspot. *Cryptog. Bryol.* 27: 141-152.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World. 14B. Tropical Rain Forest Ecosystems. Biogeographical and Ecological Studies.* Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R., Cleef, A. M., and Fulford, M. H. 1977. Studies on Colombian cryptogams II. Hepaticae: Oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales. *Proc. Kon. Ned. Acad. Wetensch., Ser. C* 80: 377-420.
- Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001a. Guide to the Bryophytes of Tropical America. *Mem. N. Y. Bot. Gard.* 86: 1-577.
- Gradstein, S. R., Griffin, D. III, Morales, M. I., and Nadkarni, N. M. 2001b. Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia* 23: 203-212.
- Gradstein, S. R., Obregon, A., Gehrig, C., and Bendix, J. 2010. 11. Tropical lowland cloud forest: A neglected forest type. In: Bruijnzeel, L. A., Scatena, F. N., and Hamilton, L. S. (eds.). *Tropical Montane Cloud Forests: Science for Conservation and Management.* Cambridge University Press, Cambridge, pp. 130-133.
- Griffin, D. III. 1979. Briofitos y Liqueños de los páramos. In: SalgadoLaboarian, M. L. (ed.). *El Medio Ambiente Paramo.* Mérida, Venezuela, pp. 79-87.
- Hastenrath, S. 1984. *The Glaciers of Equatorial East Africa.* D. Reidel Publishing Company, Dordrecht, Holland.
- Hedberg, O. 1964. Features of Afro-alpine plant ecology. *Acta Phytogeogr. Suecica* 49: 1-144.
- Hedberg, O. 1969. Evolution and speciation in a tropical high mountain flora. *Biol. J. Linn. Soc.* 1: 135-148.
- Holz, I. 2003. Diversity and Ecology of Bryophytes and Macrolichens in Primary and Secondary Montane *Quercus* Forests, Cordillera de Talamanca, Costa Rica. Ph.D. Dissertation, Georg-August-Universität zu Göttingen, Göttingen, Germany, 172 pp.
- Holz, I. and Gradstein, S. R. 2005. Phytogeography of the bryophyte floras of oak forests and páramo of the Cordillera de Talamanca, Costa Rica. *J. Biogeogr.* 32: 1591-1609.
- Karlén, W., Fastook, J. L., Holmgren, K., Malmström, M., Matthews, J. A., Odada, E., Risberg, J., Rosqvist, G., Sandgren, P., Shemesh, A., and Westerberg, L.-O. 1999. Glacier fluctuations on Mount Kenya since ~6000 Cal. Years BP: Implications for Holocene climate change in Africa. *Ambio* 28: 409-418.
- Köhler, L., Tobón, C., Frumau, K. A., and Bruijnzeel, L. S. 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. *Plant Ecol.* 193: 171-184.
- Lawton, R. 1980. Wind and the ontogeny of elfin stature in a Costa Rican lower montane rainforest. Ph.D. Diss., University of Chicago, Chicago. In: Nadkarni, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Amer. Zool.* 34: 70-78.
- Lawton, R. O. 1982. Wind stress and elfin stature in a montane rain forest tree: An adaptive explanation. *Amer. J. Bot.* 69: 1224-1230.
- Leerdam, A. van, Zagt, R. J., and Veneklaas, E. J. 1990. The distribution of epiphyte growth-forms in the canopy of a Colombian cloud-forest. *Vegetatio* 87: 59-71.
- León-Vargas, Y., Engwald, S., and Proctor, M. C. 2006. Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. *J. Biogeogr.* 33: 901-913.
- Lyford, W. H. 1969. The ecology of an elfin forest in Puerto Rico, 7. Soil, root, and earthworm relationships. *J. Arnold Arbor.* 50: 210-224.
- Mägdefrau, K. 1983. The bryophyte vegetation of the forests and páramos of Venezuela and Colombia. *Nova Hedw.* 38: 1-63.
- Mandl, N., Lehnert, M., Kessler, M., and Gradstein, S. R. 2010. A comparison of alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane forests of southern Ecuador. *Biodiv. Conserv.* 19: 2359-2369.
- Martin, P. H., Fahey, T. J., and Sherman, R. E. 2011. Vegetation zonation in a Neotropical montane forest: Environment, disturbance and ecotones. *Biotropica* 43: 533-543.
- Merlin, M. D. and Juvik, J. O. 1995. Montane cloud forest in the tropical Pacific: Some aspects of their floristics, biogeography, ecology, and conservation. In: Hamilton, L. S., Juvik, J. O., and Scatena, F. N. *Tropical Montane Cloud Forests.* Springer, New York, N. Y., pp. 234-253.
- Merwin, M. C., Gradstein, S. R., and Nadkarni, N. M. 2001. Epiphytic bryophytes of Monteverde, Costa Rica. *Trop. Bryol.* 20: 63-70.
- Nadkarni, N. M. 1984. Epiphyte biomass and nutrient capital of a Neotropical elfin forest. *Biotropica* 16: 249-256.
- Nadkarni, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. *Amer. Zool.* 34: 70-78.
- Nadkarni, N. M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica* 32: 358-363.

- Nadkarni, N. M. and Longino, J. T. 1990. Invertebrates in canopy and ground organic matter in a Neotropical montane forest, Costa Rica. *Biotropica* 22: 286-289.
- Nadkarni, N. M. and Solano, R. 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: An experimental approach. *Oecologia* 131: 580-586.
- Nadkarni, N. M., Cobb, A. R., and Solano, R. 2000. Interception and retention of macroscopic bryophyte fragments by branch substrates in a tropical cloud forest: An experimental and demographic approach. *Oecologia* 122: 60-65.
- Nadkarni, N. M., Schaefer, D. A., Matelson, T. J., and Solano, R. 2004. Biomass and nutrient pools of canopy and terrestrial components in a primary and a secondary montane cloud forest, Costa Rica. *Forest Ecol. Mgmt.* 198: 223-236.
- Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. *Bot. J. Linn. Soc.* 104: 281-291.
- Pérez, F. L. 1991. Ecology and morphology of globular mosses of *Grimmia longirostris* in the Páramo de Piedras Blancas, Venezuelan Andes. *Arct. Alp. Res.* 23: 133-148.
- Pérez, F. L. 1994. Vagrant cryptogams in a páramo of the high Venezuelan Andes. *Flora* 189: 263-276.
- Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Scient. Hung.* 26: 143-167.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 59-104.
- Pôrto, K. C. 1992. Bryoflores d'une forêt de plaine et d'une forêt d'altitude moyenne dans l'état de Pernambuco (Brasil). 2. Analyse écologique comparative des forêts. [Bryoflora of a lowland forest and submontane forest in Pernambuco state, Brazil. 2. Comparative ecological analysis of the forests.]. *Cryptog. Bryol. Lichenol.* 13: 187-219.
- Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). *Bryophyte Ecology*. Chapman and Hall, London, pp. 333-382.
- Reenen, G. B. A. van and Gradstein, S. R. 1983. Studies on Colombian cryptogams. XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. *Acta Bot. Neerl.* 32: 163-175.
- Richards, P. W. 1984. The ecology of tropical forest bryophytes. In: Schuster, R. M. (ed.). *New Manual of Bryology*. Vol. 2. Hattori Botanical Laboratory, Nichinan, pp. 1233-1270.
- Russell, K. W. and Miller, H. A. 1977. The ecology of an elfin forest in Puerto Rico, 17. Epiphytic mossy vegetation of Pico del Oeste. *J. Arnold Arbor.* 58: 1-21.
- Schnock, G. 1972. Evapotranspiration de la végétation épiphytique de la base des troncs de chêne et d'érable champêtre. *Bull. Soc. Roy. Bot. Belg.* 105: 143-150.
- Schofield, W. B. 1985. *Introduction to Bryology*. Macmillan Publishing Co., New York, 431 pp.
- Shacklette, H. T. 1966. Unattached moss polsters on Amchitka Island, Alaska. *Bryologist* 69: 346-352.
- Sillett, S. C., Gradstein, S. R., and Griffin, D. III. 1995. Bryophyte diversity of *Ficus* tree crowns from cloud forest and pasture in Costa Rica. *Bryologist* 98: 251-260.
- Simon, T. 1974. Estimation of phytomass dry-weight of epiphytic mosses at Sikfökut (near Eger, N. Hungary). *Acta Bot. Hung.* 21: 117-136.
- Smith, A. P. and Young, T. P. 1987. Tropical alpine plant ecology. *Ann. Rev. Ecol. Syst.* 18: 137-158.
- Song, L., Zhang, Y.-J., Chen, X., Li, S., Lu, H.-Z., Wu, C.-S., Tan, Z.-H., Liu, W.-Y., and Shi, X.-M. 2015. Water relations and gas exchange of fan bryophytes and their adaptations to microhabitats in an Asian subtropical montane cloud forest. *J. Plant Res.* 128: 573-584.
- Stadtmüller, T. 1987. *Cloud forests in the humid tropics*. United Nations University, Costa Rica, 81 pp.
- Veneklaas, E. J., Zagt, R. J., Leerdam, A. van, Ek, R. van, Brockhoven, A. J., and Genderen, M. van. 1990. Hydrological properties of the epiphyte mass of a montane tropical forest, Colombia. *Vegetatio* 89: 183-192.
- Vitt, D. H. 1991. Distribution patterns, adaptive strategies, and morphological changes of mosses along elevational and latitudinal gradients on South Pacific Islands. In: Nimis, P. L. and Crovello, T. J. (eds.). *Quantitative Approaches to Phytogeography*. Springer, Dordrecht, pp. 205-231.
- Wikipedia. 2018b. Climate of Mount Kenya. Updated 27 February 2018. Accessed 18 March 2018 at <https://en.wikipedia.org/wiki/Climate_of_Mount_Kenya>.
- Wuethrich, B. 1993. Forests in the clouds face stormy future. *Sci. News* 114: 23.
- Zotz, G. 1999. Altitudinal changes in diversity and abundance of non-vascular epiphytes in the tropics – an ecological and ecophysiological explanation. *Selbyana* 20: 257-260.
- Zotz, G., Büde, B., Meyer, A., Zellner, H., and Lange, O. L. 1997. Water relations and CO₂ exchange of tropical bryophytes in a lower montane rainforest in Panama. *Bot. Acta* 110: 9-17.

CHAPTER 8-11

TROPICS: HYDRIC AND XERIC HABITATS

TABLE OF CONTENTS

Inundated Forests.....	8-11-2
Várzea and Igapó Forests.....	8-11-2
Floodplains and Mangrove Forests.....	8-11-4
Pirizal.....	8-11-8
Peatlands.....	8-11-8
Aquatic.....	8-11-11
Rheophytes.....	8-11-12
Lakes.....	8-11-16
Seepage Areas.....	8-11-20
Xeric Habitats.....	8-11-21
Savannahs.....	8-11-24
Succession.....	8-11-25
Life Cycle Strategies.....	8-11-26
Tropical Deserts.....	8-11-27
Summary.....	8-11-31
Acknowledgments.....	8-11-31
Literature Cited.....	8-11-31

CHAPTER 8-11

TROPICS: HYDRIC AND XERIC HABITATS



Figure 1. Várzea in Brazil. Photo by D. N. Santos, through Creative Commons.

Inundated Forests

The classification of inundated forests has been inconsistent even by botanists, particularly in different regions (Prance 1980), making descriptions of the vegetation based on literature difficult and confusing. Prance divided these forests into periodically inundated (seasonal várzea, seasonal igapó, mangrove, tidal várzea, flood plain forest) and permanently waterlogged (permanent white water swamp forest, permanent igapó).

Inundated forests are forests that are constantly or periodically in water and include the **igapós** (Figure 2-Figure 3) and **várzeas** (Figure 1, Figure 7) (Pires & Prance 1985). These flood forests cover 2% or more of Brazilian Amazonia, excluding the rivers themselves. For example, the palm *Astrocaryum jauari* is, in various places, flooded 30-340 days a year (Piedade *et al.* 2005, 2006). The **igapós** are black and clearwater areas, whereas the **várzeas** are muddy waters. In the black and clearwater areas, the **igapó**

gives the water a golden appearance (Figure 4) (Pires & Prance 1985). In flood season, the igapó trees are flooded so that their trunks are completely submerged (Figure 5), permitting one to canoe through the canopy (Figure 6).

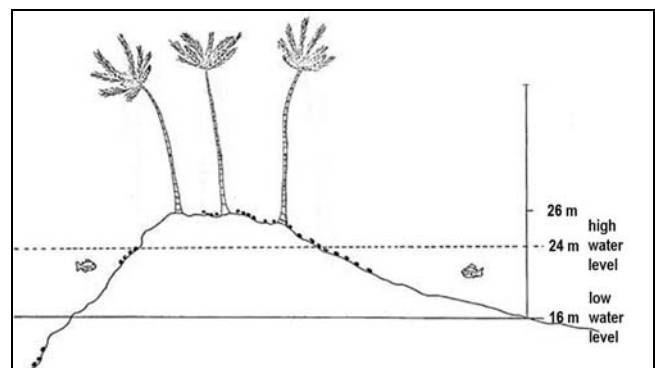


Figure 2. Diagram of igapó showing water level fluctuation for a mound of trees. Modified from Piedade *et al.* 2006.



Figure 3. Flooded igapó forest in Black River of Anavilhana, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.



Figure 6. Canoeing through canopy of flooded igapó forest in Black River of Anavilhana, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.



Figure 4. Golden water in flooded igapó forest in Black River of Novo Airão, state of Amazonas, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.



Figure 5. Flooded igapó forest in Black River of Anavilhana, Brazil, in 2014. Photo courtesy of Tatiany Oliveira da Silva.

Várzea and Igapó Forests

The classification of Amazonian floodplains is based on water and vegetation types (Ferreira *et al.* 2005, 2013). The **igapó** (Figure 8) and **várzea** (Figure 1, Figure 7) are the most common of these. The **várzea** is a seasonally whitewater-flooded forest growing along rivers in the Amazon. The **igapó** forests are seasonally inundated with freshwater and typically occur along the lower reaches of rivers and around freshwater lakes, whereas the **permanent igapó** forest is in water year-round, but with fluctuating water levels.

Using 100 plots, each of 20 x 20 m, within 4 hectares, Ferreira and coworkers (2013) identified all trees and lianas greater than 10 cm diameter at breast height. They identified a total of 97 species, with 75 in igapó and 48 in várzea forests. Only 26 species occurred in both forests, indicating that these are distinct forests. The várzea forests have more soil nutrients, more light availability, and greater natural disturbance, perhaps helping to explain the plant diversity differences.



Figure 7. Várzea forest, Marajó, Brazil. Photo by Dayse Ferreira, through Creative Commons.



Figure 8. Igapó in Brazil. Photo by Lisa Cyr, through Creative Commons.

Cerqueira *et al.* (2017) studied the epiphytic bryophytes on *Virola surinamensis* (baboonwood; Figure 9) in igapó (Figure 8) and várzea (Figure 7) forests in the Caxiuanã National Forest. They found a greater richness in the igapó forest (44 species) compared to that of the várzea forest (38 species) (Figure 10). Furthermore, the composition of the bryophyte communities differed between the várzea and the igapó, but did not differ between dry and rainy periods. Although Cerqueira *et al.* (2016) studied only seven species in detail, two species were associated with the forest type and two species to the seasonality of flooding. They identified 54 bryophyte species in 502 samples; 34 were fertile. Sexual reproduction predominated over asexual (Figure 10).



Figure 9. *Virola surinamensis*, an igapó substrate for bryophytes. Photo by Reinaldo Aguilar, through Creative Commons.

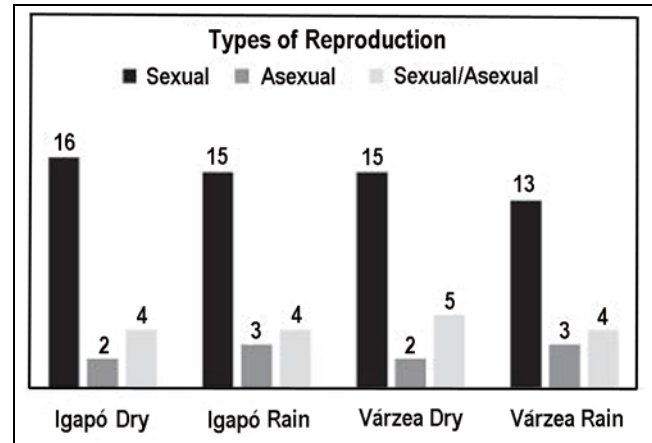


Figure 10. Reproduction of bryophytes in inundated forests. Numbers refer to number of species. Modified from Cerqueira *et al.* 2016.

Lopes *et al.* (2016) compared the bryophyte communities as they relate to degrees of flooding in the igapó and várzea. They sampled eighteen transects each in the igapó and várzea forests of São Domingos do Capim, Pará State, Brazil. As in many rainforest studies, they found that the leafy liverwort family **Lejeuneaceae** (Figure 28) was the predominant family, with 63 species. Among the mosses, the **Calymperaceae** (Figure 11, Figure 30) had the most species, with 8 species. In total, they reported 118 bryophyte species, 82 liverworts and 37 mosses. Live bark was the most colonized substrate, with 45 species exclusive to it, but 101 species in total on bark. Decomposing bark followed, with 66 species, 16 of which were exclusive to it.

Floodplains and Mangrove Forests

Mangrove forests and floodplains are subject to inundation by salt water (Pires & Prance 1985). They are species-poor and typically quite uniform. Among the primary tree species is the mangrove, ***Rhizophora mangle*** (Figure 12).

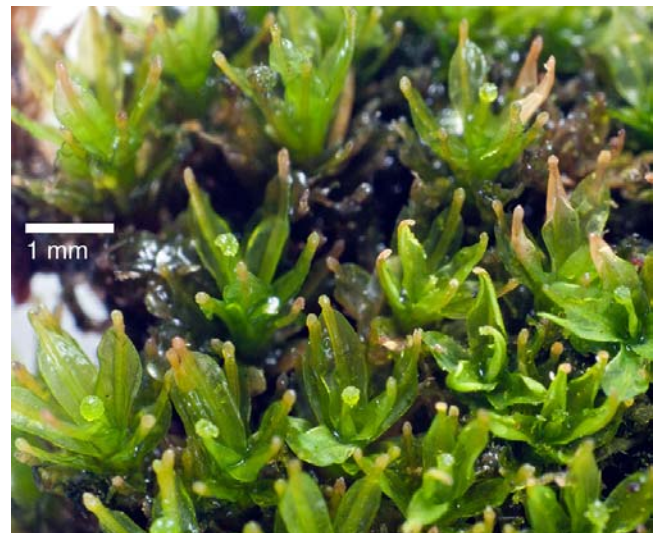


Figure 11. *Calymperes tenerum*, one of the common species on mangroves in eastern Thailand. Photo from Auckland Museum, through Creative Commons.

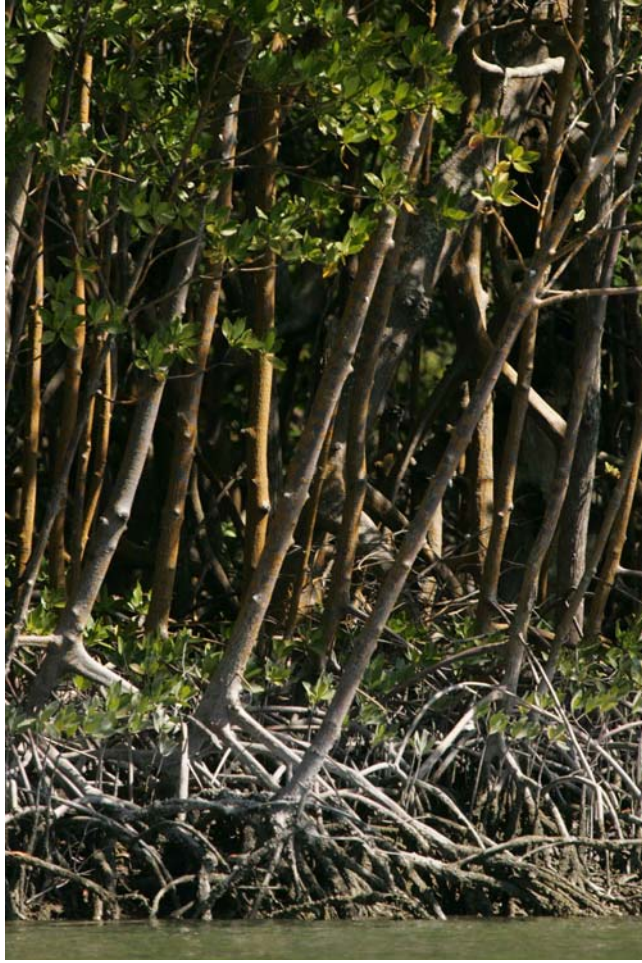


Figure 12. *Rhizophora mangle*, a primary species of the mangrove forest. Photo by Steve Hillebrand, through public domain.

In Thailand there are about 40 tree species in the mangrove forests (Thaithong 1984). Among these, only 10 species support epiphytic bryophytes. Thaithong found only 5 species of mosses and 21 species of leafy liverworts. *Rhizophora apiculata* (Figure 13) was the most favorable phorophyte for bryophyte species richness, with 23 bryophyte species found on this host. She found 22 of the 111 specimens of bryophytes belong to only 5 species of mosses [*Calymperes tenerum* (Figure 11), *Calymperes hampei*, *Octoblepharum albidum* (Figure 14), *Leucophanes albescens* (see Figure 15), and *Dixonia orientalis*]. The remaining 89 specimens were represented by 21 species of leafy liverworts in the genera *Frullania* (Figure 26), *Lejeunea* (Figure 16), *Acrolejeunea* (Figure 17-Figure 18), *Mastigolejeunea* (Figure 19), *Lopholejeunea* (Figure 20), *Pycnolejeunea* (Figure 21), *Thysananthus* (Figure 22), *Schiffneriolejeunea* (Figure 23), *Caudalejeunea* (Figure 24), and *Cololejeunea* (Figure 25). The most common bryophytes, occurring in both the eastern and western mangrove forests, were *Frullania meyeniana* (Figure 26), *Acrolejeunea fertilis* (Figure 27), *Cheilolejeunea intertexta* (Figure 28), and *Lopholejeunea subfusca* (Figure 29), all leafy liverworts and all but *Frullania* in the *Lejeuneaceae*. In the eastern mangrove forests, the moss *Calymperes tenerum* (Figure 11) is also common, whereas in the western mangroves *Calymperes erosum* (Figure 30) is common.



Figure 13. Mangrove of *Rhizophora apiculata*, a favorable host for bryophytes in Thailand. Photo by Bernard Dupont, through Creative Commons.



Figure 14. *Octoblepharum albidum*, a common species in the mangrove forests of Thailand. Photo by Bramadi Arya, through Creative Commons.



Figure 15. *Leucophanes* sp.; *Leucophanes albescens* is one of five species of mosses in the mangrove forests of Thailand. Photo by Neils Klazenga, with permission.



Figure 16. *Lejeunea flava*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Scott Zona, through Creative Commons.

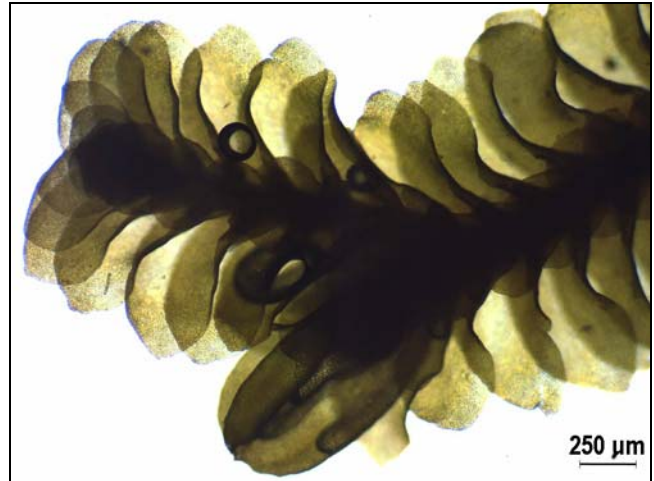


Figure 19. *Mastigolejeunea auriculata*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Blanka Aguero, with permission.



Figure 17. *Acrolejeunea fertilis*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for non-commercial use.



Figure 20. *Lopholejeunea subfusca*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Yang Jia-dong, through Creative Commons.



Figure 18. *Acrolejeunea fertilis*, in a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Heino Lepp, Australian National Botanic Gardens, with permission only for non-commercial use.



Figure 21. *Pycnolejeunea pilifera*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.



Figure 22. *Thysananthus repletus* from China, in a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Y. M. Wei, courtesy of Robbert Gradstein.



Figure 25. *Cololejeunea cardiocarpa*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Paul Davison, with permission.



Figure 23. *Schiffneriolejeunea polycarpa*, in a common leafy liverwort genus in the mangrove forests of Thailand. Photo from <docencia.udea.edu.co>, with implied permission.



Figure 26. *Frullania meyeniana*, one of common species on *Rhizophora apiculata*. Photo by Scott Zona, through Creative Commons.



Figure 24. *Caudalejeunea lehmanniana*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by Scott Zona, with permission.



Figure 27. *Acrolejeunea fertilis*, one of common species on *Rhizophora apiculata*. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.



Figure 28. *Cheilolejeunea intertexta*, a species common on *Rhizophora apiculata* in Malaysia. Photo from Wilding *et al.* 2016, with permission.



Figure 29. *Lopholejeunea subfusca*, one of the common species on *Rhizophora apiculata*. Photo by Yang Jia-dong, through Creative Commons.



Figure 30. *Calymperes erosum*, one of the common species on mangroves in western Thailand. Photo by Li Zhang, with permission.

Frangi and Lugo (1992) used 10-year-old wooden stakes to examine bryophytes on the microtopographic gradient of a floodplain forest in the Luquillo Experimental Forest, Puerto Rico. They assessed biomass and nutrients, finding 210-1400 kg ha⁻¹ of ash-free biomass. Nutrient levels for bryophytes in the floodplain floor in kg ha⁻¹ were N (9.1), P (0.5), K (3.3), Ca (1.7), Mg (1.7), Mn (0.33), Fe

(11.6), and Al (13.8). These accumulations are in the same order of magnitude as those of the fine litter, suggesting passive accumulation. On streambank slopes or slopes of tree mounds, the biomass and nutrient accumulation were greater than in other microhabitats. Frangi and Lugo concluded that the floodplain bryophytes serve as biotic filters of flood waters, helping in retention of nutrients in these habitats.

Studies on bryophytes of tropical floodplains and mangrove forests seem to be minimal. Yamaguchi *et al.* (1987) listed the terrestrial bryophytes in mangrove forests of Japan. Windolf (1989) analyzed the bryophyte species in sub-tropical mangroves in southern Queensland, Australia. Windolf made 337 collections and described the host-substrate relationship, comparing bryophyte occurrences to those on the adjacent non-mangrove trees. There seems to be an absence of ecological studies for this habitat.

Hydropogon fontinaloides occurs in periodically inundated locations in the Orinoco and Amazon River floodplains (Mägdefrau 1973).

Pirizal

The **pirizal** vegetation occurs only in small, restricted areas. These are shallow lakes or puddles and the water is stagnant, dark, and transparent. This tropical habitat is not typically a habitat for bryophytes.

Peatlands

Gates (1915) reported on *Sphagnum* (Figure 31-Figure 33) bogs in the tropics, noting that these had only been described from higher altitudes. Eddy (1977) provided a treatment of the *Sphagnum* species of tropical Asia.

McQueen (1991) considered the *Sphagnum*-dominated peatlands in southern Ecuador to be similar to the intermediate or transitional poor fens in the Northern Hemisphere, based on levels of pH, conductivity, and concentrations of Fe, K, Mg, Mn, Na, and P. Species included *S. magellanicum* (Figure 31), *S. recurvum* (Figure 32), *S. sancto-josephense*, and *S. denticulatum* (Figure 33).



Figure 31. *Sphagnum magellanicum*, a species found in *Sphagnum*-dominated peatlands in southern Ecuador. Photo by Michael Lüth, with permission.



Figure 32. *Sphagnum recurvum*, a species found in *Sphagnum*-dominated peatlands in southern Ecuador. Photo by Malcolm Storey, <www.discoverlife.com> through Creative Commons.



Figure 33. *Sphagnum denticulatum*, a species found in *Sphagnum*-dominated peatlands in southern Ecuador. Photo by Michael Lüth, with permission.

Wolfe and McQueen (1992) noted that few tropical studies of *Sphagnum* (Figure 31-Figure 33) habitats had been published and that these were restricted to the páramo in the northwestern part of South America. Cleef (1981) distinguished four kinds of *Sphagnum* bogs in the Cordillera Oriental of Colombia, distinguished on the basis of vegetation, pH, altitude, and peat depth. In addition, Cleef described *Sphagnum* habitats including wet seeps, peaty lake shores, floating mats, and boggy glacial valleys at 3,600-3,850 m asl.

Peatlands are not always *Sphagnum* (Figure 31-Figure 33) habitats. In the high elevation tropical Andes of Colombia, similar conditions to those of *Sphagnum* bogs prevail, but these peatlands are *Distichia muscoides* (Juncaceae – rushes; Figure 34) cushion bogs. These cushions provide similar function and structure to those of *Sphagnum* in boreal and austral regions (Cleef 1981; Fritz *et al.* 2011). Even the dead parts of these cushions fall to the bottom of the pool and are converted to turf, as does *Sphagnum* (Cuatrecasas 1968). In the high Andes, such cushion plants are restricted to areas with poor drainage or that have a positive water balance (Cleef 1981; Kleinebecker *et al.* 2010). Benavides *et al.* (2013) concluded that cushion plants are "capable of reducing

methane emission on an ecosystem scale by thorough soil and methane oxidation," whereas *Sphagnum* lawns had substantial methane emissions. These mountaintop peatland habitats are in danger of extinction under most climate change scenarios (Colwell *et al.* 2008; Ruiz *et al.* 2008).



Figure 34. *Distichia muscoides*, a member of the rush family Juncaceae that resembles moss cushions and is forming a cushion bog like those found in the Andes. Photo by Sergej – Bofedal, through Creative Commons.

Likewise, despite geographic differences, the niche width and overlap values of *Sphagnum* (Figure 31, Figure 35) species in tropical Costa Rica are similar to those for *Sphagnum* species in North America (McQueen 1995). In Costa Rica, *S. magellanicum* (Figure 31) and *S. sparsum* have the broadest niche widths. Despite its relatively narrow niche with, *S. sancto-josephense* is one of the most common *Sphagnum* species accompanying the other two. The niche overlap values are high, except for that of *S. platyphyllum* (Figure 35). This species occurs in habitats rich in iron. The pH, conductivity, and concentrations of Ca, Fe, K, Mg, Mn, Na, and P in these peatlands are similar to those of the páramo habitats in South America.



Figure 35. *Sphagnum platyphyllum*, a species with small niche overlap in Costa Rica. Photo by Michael Lüth, with permission.

In Bolivia, McQueen (1997) determined that, based on pH, conductivity, and concentrations of Ca, K, Mg, Na, and P, the *Sphagnum* habitats in páramo and cloud forests of the Bolivian Andes are ombrotrophic. In these habitats, the *Sphagnum* forms small, scattered carpets. The species include those from Ecuador and Costa Rica. Common species are *S. alegrense*, *S. boliviae*, *S. cuspidatum* (Figure 36), *S. magellanicum* (Figure 31), *S. oxyphyllum*, *S. recurvum* (Figure 32), *S. sancto-josephense*, and *S. sparsum*.



Figure 36. *Sphagnum cuspidatum*, a common species in the páramo and cloud forests of the Bolivian Andes. Photo by Michael Lüth, with permission.

Bosnian *et al.* (1993) described cushion mires in the páramo. Two types are dominated by tracheophytes, with *Campylopus reflexisetus* (Figure 37) occurring on the cushions. Two are dominated by bryophytes. The mosses *Sphagnum sparsum*, *Breutelia* sp. (Figure 38), and *Campylopus cuspidatus* var. *dicnemoides* (Figure 39) dominate one of these, and the leafy liverwort *Lophonardia laxifolia* along with the tracheophyte *Cortaderia sericantha* (Figure 40) dominate the other. The *Sphagnum sparsum* type requires higher conductivity of ground water, higher NO₃ and PO₄ levels, and lower Fe levels. The *Lophonardia laxifolia* type requires lower levels of K and Al. A fifth type is dominated by submerged *Sphagnum cyclophyllum* (Figure 41), whereas the sixth has only the aquatic vegetation of *Equisetum bogotense* (Figure 42) and algae. Moss cover is low in the water-filled depressions among the cushions.



Figure 37. *Campylopus reflexisetus*, a species that occurs on tracheophyte cushions in cushion mires of the South American páramo. Photo by Michael Lüth, with permission.



Figure 38. *Breutelia*, one of the dominant mosses in one type of cushion mire in the páramo. Photo through Creative Commons.



Figure 39. *Campylopus cuspidatus*, one of the dominant mosses in one type of cushion mire in the páramo. Photo by Michael Lüth, with permission.



Figure 40. *Cortaderia selloana* in Brazil; *Cortaderia sericantha*, along with the liverwort *Lophonardia laxifolia*, dominates one of the moss-dominated cushion mires in the páramo. Photo by H. M. Longhi-Wagner, through Creative Commons.



Figure 41. *Sphagnum cyclophyllum*, the dominant species in one type of cushion mire in the páramo. Photo by Blanka Agüero, with permission.



Figure 42. *Equisetum bogotense*, the dominant plant in one type of cushion mire in the páramo. Photo by Penarc, through public domain.

Liu *et al.* (2014) examined population structure of *Sphagnum tumidulum* (Figure 43) on tropical Reunion Island. Using genotypes at 10 microsatellite loci, they determined the species to be highly variable. They identified 31 multilocus genotypes. This variability suggests that sexual reproduction is successful on the island, although capsules have not been found. On the other hand, gene flow among populations appears to be very limited.



Figure 43. *Sphagnum tumidulum*, a common species on tropical Reunion Island. Photo by courtesy of Jacques Bardat.

Oxygen deficiency is important for the survival of *Sphagnum* spores (Figure 44) (Feng *et al.* 2018). After 60 days of storage, those spores that experienced oxygen injection had lower germinability than those that lacked it. High pH further diminished the germinability. These requirements make *Sphagnum* peat suitable substrate for retaining viable spores.

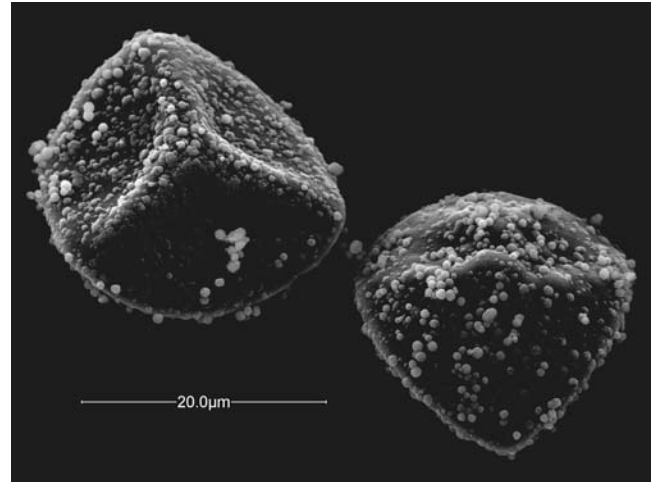


Figure 44. *Sphagnum* spores SEM. Photo from Whitaker & Edwards 2010, with permission from Diane Edwards.

Aquatic

In the tropics, aquatic bryophytes grow in periodically inundated habitats such as river beds, marshes, and waterfalls (Gradstein *et al.* 2018). Permanently submerged bryophytes are rare, occurring primarily at high altitudes. Their modifications of morphological traits (de Winton & Beever 2004; Rankin *et al.* 2017), sometimes induced by changing water conditions, make identification difficult.

Lowland tropical habitats are especially challenging for bryophytes. Because the bryophytes are continuously hydrated, they continue respiration even when the temperatures are high. This results in net carbon loss as respiration exceeds photosynthesis, especially in low light conditions.

The red-listed liverwort *Colura irrorata* (Figure 45) was known only from its type collection from the Ecuadorian Andes in 1857 (Gradstein *et al.* 2004). But Gradstein and coworkers found the species along two tributaries of the Rio Pastaza, Ecuador. It is in fact abundant along the Rio Topo, where it lives on the periodically submerged *Cuphea bombonasa* (Figure 45) shrubs along with the rare *Myriocoleopsis gymnocolea* (see Figure 46). In the Ecuadorian Andes, *Colura irrorata* occurs almost exclusively on the small, woody subshrub *Cuphea bombonasa* where it is very close to torrential water (Gradstein & Benitez 2014). Three other rare rheophytic bryophytes [*Lejeunea topoensis* (see Figure 47), *Myriocoleopsis gymnocolea*, and *Sematophyllum steyermarkii* (see Figure 48)] typically occur with it. The species *Colura irrorata* is distinguished by a very high number of clustered gynocidia as well as numerous antheridia per male bract (Gradstein *et al.* 2004).



Figure 45. *Colura irrorata*, showing numerous gynoecia, growing on stems of *Cuphea bombonae* along the Numpatakaima river at 1,540 m asl. Photo by Lou Jost, EcoMinga, with permission.



Figure 46. *Myriocoleopsis minutissima*; *Myriocoleopsis gymnocolea* is one of the rare rheophytic liverworts in the Ecuadorian Andes. Photo by Hugues Tinguy, through Creative Commons.



Figure 47. *Lejeunea cavifolia*; *Lejeunea topoensis* is one of the rare rheophytic liverworts in the Ecuadorian Andes. Photo by Hermann Schachner, through Creative Commons.



Figure 48. *Sematophyllum* sp. from the Neotropics; *Sematophyllum steyermarkii* is one of the rare rheophytic liverworts in the Ecuadorian Andes. Photo by Michael Lüth, with permission.

Rheophytes

Our knowledge of bryophytic **rheophytes** (aquatic plant that lives in fast moving water currents) in the tropics is somewhat limited. It is greater for Asia than for Africa or South America (Shevock *et al.* 2017). In Malesia, studies of floristic works have elaborated the bryophytes of such habitats (Koponen & Norris 1983; Eddy 1988, 1990, 1996). In Borneo Island, bryophytes are species rich above 1,000 m asl. In lower elevations, heavy deposits of sediments can be detrimental to rheophytic bryophytes.

The seemingly ever-present **Lejeuneaceae** even ventures into rheophytic habitats. Reiner-Drehwald (1999) reported *Potamolejeunea polyantha* [now considered to be a subgenus of *Lejeunea* (Gradstein & Reiner-Drehwald 2007)] as a rheophyte from South America, noting that it was poorly known.

At higher elevations, one can find *Neckeropsis beccariana* (see Figure 49), *Thamnobryum ellipticum* (see Figure 50), and *Fissidens beccarii* (see Figure 51) on boulders; *Calymperes tahitense* (see Figure 52) occurs on hardwood branches or exposed tree roots; and *Sclerohyllum littorale* on branches of rheophytic shrubs (Akiyama 1992a). In a separate paper, Akiyama (1992b) described the morphology and ecology of these rheophytes. Along the river and streambanks, one can find carpets of bryophytes that are actually rheophytic, surviving high water levels and rapid flow (Ma *et al.* 2014). Above this flooding zone, the same shrub species lack these rheophytic bryophytes. In many areas of the tropics, these bryophytes are submerged multiple times through the year, especially during monsoon season.



Figure 49. *Neckeropsis lepineana*; *Neckeropsis beccariana* occurs at higher elevations on boulders. Photo by Li Zhang, with permission.



Figure 50. *Thamnobryum neckeroides*; *Thamnobryum ellipticum* occurs at higher elevations on boulders. Photo by Blanka Agüero, with permission.



Figure 51. *Fissidens marthae*; *Fissidens beccarii* occurs at higher elevations on boulders. Photo by Jan-Peter Frahm, with permission.

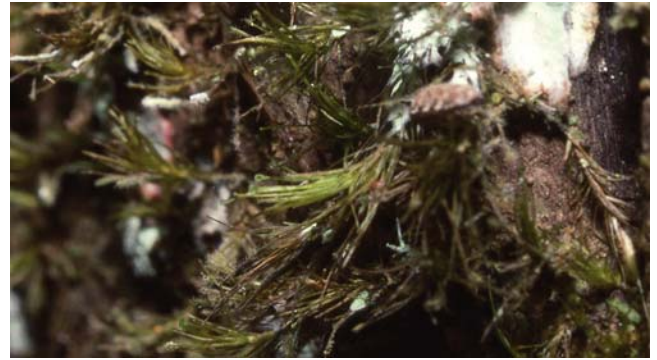


Figure 52. *Calymperes* sp. from Toro Negro, Puerto Rico. *Calymperes tahitense* occurs on hardwood branches or exposed tree roots. Photo by Janice Glime.

Despite the cosmopolitan nature of many rheophytes in the temperate zone, new tropical species are still awaiting exploration. For example, Shevock *et al.* (2011) named *Yunnanobryon* as a new genus of rheophytic moss from southwest China. *Yunnanobryon rhyacophilum* (Figure 53-Figure 54) occurs in fast-flowing rivers. As is typical of mosses in fast-flowing water, it is pleurocarpous. It is slender with stoloniform primary stems and intricately much-branched secondary stems that become flagellate-attenuate at the tips.



Figure 53. *Yunnanobryon rhyacophilum* with developing young leaves in a stream in Yunnan, China. Photo by Jim Shevock, with permission.



Figure 54. *Yunnanobryon rhyacophilum* from a stream in Yunnan, China. Photo by Li Zhang, with permission.

Neotropical bryophyte families with at least some species that can be found as rheophytes include the mosses **Amblystegiaceae** (Figure 78, Figure 81), **Andreaeaceae** (Figure 55), **Brachytheciaceae** (Figure 56), **Fissidentaceae** (Figure 51), **Hydropogonaceae**, **Leucomiaceae** (Figure 57), **Pilotrichaceae** (Figure 58), **Pottiaceae** (Figure 86-Figure 87), **Seligeriaceae** (Figure 76), **Sematophyllaceae** (Figure 48), **Sphagnaceae** (Figure 31-Figure 33, Figure 35-Figure 36), and the liverworts **Aneuraceae** (Figure 73), **Balantiopsidaceae** (Figure 70), **Cephaloziellaceae** (Figure 59), **Fossombroniaceae** (Figure 62-Figure 63), **Jungermanniaceae** (Figure 75), **Lejeuneaceae** (Figure 27-Figure 29), **Lophocoleaceae** (Figure 60), and **Pelliaceae** (Figure 61) (see Mägdefrau 1973; Griffin *et al.* 1982; Bartlett & Vitt 1986; Gradstein & Vána 1999; Reiner-Drehwald 1999; Gradstein *et al.* 2001a, 2004, 2011; Gradstein & Reiner-Drehwald 2007; Hedenäs 2003; Crandall-Stotler & Gradstein 2017). Permanent submergence is less common in the tropics compared to temperate and Arctic zones (Gradstein *et al.* 2018).



Figure 55. *Andreaea nivalis* (**Andreaeaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Michael Lüth, with permission.



Figure 56. *Platyhypnidium riparioides* (**Brachytheciaceae**). Some members of this family are among the Neotropical rheophytes. Photo from Proyecto Musgo through Creative Commons.



Figure 57. *Leucomium strumosum* (**Leucomiaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Claudio Delgadillo Moya, with permission.



Figure 58. *Cyclodictyon laetevirens* (**Pilotrichaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Jan-Peter Frahm, with permission.



Figure 59. *Cephaloziella dentata* (**Cephaloziellaceae**). Some members of this family are among the Neotropical rheophytes. Photo by Des Callaghan, with permission.

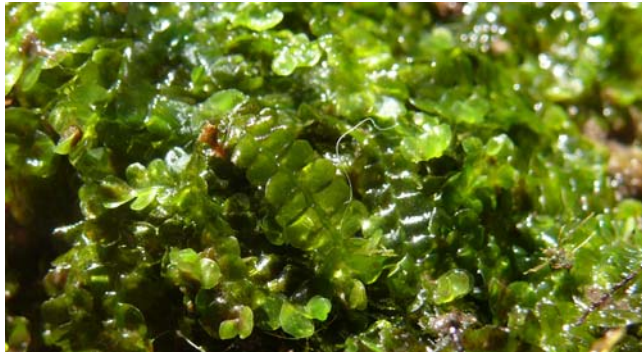


Figure 60. *Chiloscypus polyanthos* (Lophocoleaceae). Some members of this family are among the Neotropical rheophytes. Photo by Bernd Haynold through Creative Commons.



Figure 61. *Pellia endiviifolia* (Pelliaceae). Some members of this family are among the Neotropical rheophytes. Photo by Janice Glime.

Gradstein and Reiner-Drehwald (2007) described a new rheophytic liverwort, *Lejeunea topoensis* (Figure 16), from the Andes in Ecuador and southern Brazil. Crandall-Stotler and Gradstein (2017) found a new riverine species in Ecuador, *Fossombronia jostii* (Figure 62). It seems to be restricted to limestone boulders, where one can also find *F. texana* (Figure 63) and *F. wrightii*. These species experience major flooding events that appear to wipe out the entire population, but given a little time, these species return, regenerating from remaining shoot apices of plants that have otherwise been killed by the flooding.



Figure 62. *Fossombronia jostii* resprouting on limestone rocks in Ecuador after flooding. Photo by Lou Jost, EcoMinga, with permission.

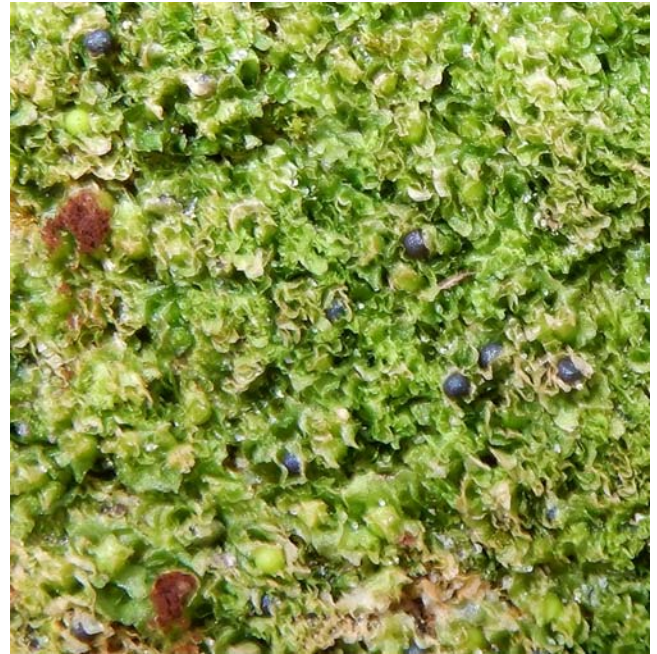


Figure 63. *Fossombronia texana*, one of the species on the limestone rocks in Ecuador. Photo by Bob O'Kennon, through Creative Commons.

Racomitrium lamprocarpum (= *Bucklandiella lamprocarpa*; Figure 64) is a rheophytic moss from the central and northern Andean countries (Bednarek-Ochyra 2015). Ochyra concluded that *Racomitrium bartramii* should be included within this species. *Racomitrium lamprocarpum* is an austral cool-adapted species that has spread deep into the tropics, where it finds suitable habitat at high elevations in the Neotropics and in East and Central Africa.



Figure 64. *Racomitrium lamprocarpum*, Cape Horn, a rheophyte in both Africa and the Neotropics. Photo by Juan Larrain, through Creative Commons.

Ochyra *et al.* (1998) reported a new moss species from subtropical Tenerife as *Gradsteinia torrenticola*, considering it to be most closely related to the Andean *Gradsteinia andicola* from Colombia. But instead it was later placed in *Platyhypnidium* (*P. torrenticola*; Figure 65) (Ochyra & Bednarek-Ochyra 1999). In the Neotropics, *Platyhypnidium torrenticola* is known only from a single waterfall.



Figure 65. *Platyhypnidium torrenticola*, a species from waterfall habitats in Colombian Andes. Photo by BBS website, with permission from Barry Stewart.

So why are we seeing so many new species in a relatively restrictive habitat? Gradstein *et al.* (2011) attributed the unusual morphology of river bank species to habitat specialization and isolation. Such is the case for *Cololejeunea stotleriana* (Figure 66) from Ecuador. This species is both rheophilous and epiphytic. It was the first member of the subgenus *Chlorolejeunea* to be found in the Neotropics, with the other known member occurring in Asia. Furthermore, it occurs with the rare mosses *Fissidens hydropogon* (Figure 67) and *Lepidopilum caviusculum* (Figure 68), both previously known only from their type collections 150 years ago. But rarity and new species are probably products of the isolation between mountaintops, with unsuitable habitat in between.



Figure 66. *Cololejeunea stotleriana* on a fern frond. Photo by F. Werner, courtesy of Robbert Gradstein.



Figure 67. Herbarium specimen of *Fissidens hydropogon*, a rare rheophilic moss from Ecuador. Photo from Alchetron.com, through Creative Commons.



Figure 68. Herbarium specimen of *Lepidopilum caviusculum*, a rare rheophilic moss from Ecuador. Photo Natural History Museum, London, through Creative Commons.

Lakes

Like the rheophytic habitat, Andean and other high-altitude lakes are isolated from those on surrounding mountains by inhospitable habitat surrounding them. Since aquatic bryophytes are transported mostly by fragments, this effectively isolates them.

In high altitude lakes in the Neotropics, one can find the liverworts *Clasmatocolea vermicularis* (Figure 69), *Gymnocoleopsis cylindriformis*, *Herbertus sendtneri* (Figure 83), *Isotachis obtusa* (Figure 70), *Jensenia spinosa* (Figure 71), *Lophonardia laxifolia*, *Marchantia pilcata* (Figure 72), *Riccardia cataractarum* (see Figure 73), *Ricciocarpos natans* (Figure 74), and *Syzygiella*

sonderi (see Figure 75) (Gradstein *et al.* 2018; see also Cleef 1981; Gradstein *et al.* 2001b; Hedenäs 2003; Churchill 2018). Mosses include *Blindia gradsteinii* (see Figure 76), *Ditrichum submersum* (see Figure 77), *Drepanocladus* spp. (Figure 78), *Fontinalis bogotensis* (see Figure 79), *Gradsteinia andicola*, *Philonotis andina* (see Figure 80), *Pseudocalliergon* spp. (Figure 81), *Scorpidium* spp. (Figure 82), and *Sphagnum* spp. (Figure 31-Figure 33). Most of the mosses and all of the liverworts also can grow out of water in wet situations. Only the mosses *Blindia gradsteinii*, *Ditrichum submersum*, *Fontinalis bogotensis*, and possibly some *Sphagnum* species are restricted to submergence. *Blindia gradsteinii* is known from only one locality, a small pond at 4,090 m asl in the páramo de Sumapaz in Colombia (Churchill 2016). *Gradsteinia andicola* has been found only once, in a dried-up lake at 3,650 in the same páramo (Gradstein *et al.* 2018). These two rare species suggest that they are restricted by temperature.



Figure 69. *Clasmatocolea vermicularis*, a leafy liverwort from high altitude lakes in the Neotropics. Photo by John Engel, through Creative Commons.



Figure 70. *Isotachis* sp. from the Neotropics. *Isotachis obtusa* occurs in high-altitude lakes in the Neotropics. Photo by Michael Lüth, with permission.



Figure 71. *Jensenia spinosa*, a liverwort from high altitude lakes in the Neotropics. Photo by Jan-Peter Frahm, with permission.



Figure 72. *Marchantia plicata*, a liverwort from high altitude lakes in the Neotropics. Photo by Jan-Peter Frahm, with permission.



Figure 73. *Riccardia* sp. from the Neotropics. *Riccardia cataractarum* is a liverwort from high altitude lakes in the Neotropics. Photo by Michael Lüth, with permission.



Figure 74. *Ricciocarpos natans*, a liverwort from high altitude lakes in the Neotropics. Photo by Jan-Peter Frahm, with permission.



Figure 75. *Syzygiella autumnalis*; *Syzygiella sonderi* is a liverwort from high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.



Figure 76. *Blindia acuta*; *Blindia gradsteinii* is a moss from high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.



Figure 77. *Ditrichum gracile*; *Ditrichum submersum* is a moss from high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.



Figure 78. *Drepanocladus aduncus*; several species of *Drepanocladus* s.l. occur in high altitude lakes in the Neotropics. Photo by Hermann Schachner, through Creative Commons.



Figure 79. *Fontinalis antipyretica*; *Fontinalis bogotensis* is a moss from high altitude lakes in the Neotropics. Photo by Malcolm Storey <DiscoverLife.com>, through online permission.



Figure 80. *Philonotis* sp. from the Neotropics; *Philonotis andina* is a moss from high altitude lakes in the Neotropics. Photo by Michael Lüth, with permission.



Figure 81. *Pseudocalliergon trifarium*; members of this genus occur in high altitude lakes in the Neotropics. Photo by Blanka Agüero, with permission.



Figure 82. *Scorpidium scorpioides*; members of this genus occur in high altitude lakes in the Neotropics. Photo by David T. Holyoak, with permission.

In the Andes of Colombia, at 4,120 m asl, Gradstein *et al.* (2018) found a large population of *Herbertus sendtneri* (Figure 83) in a glacial lake. The researchers speculated that a rock-inhabiting population had washed into the lake by vegetative branches or other fragments.



Figure 83. *Herbertus sendtneri*, a species found in a glacial lake of the Colombian Andes. Photo by Michael Lüth, with permission.

In seven páramo lakes above 3,800 m asl on Volcán Chiles, Ecuador, Terneus (2001) found that moss species (not including *Sphagnum*) were the most abundant and most frequent vegetation, exhibiting a 71.4% frequency among the lakes and a 70% frequency among the transects. They provided a mean cover of 26.7% and occupied maximum depths greater than 100 m. They had a wide depth range (>100 m) compared to other vegetation types.

In Lake Titicaca in the Andes on the border of Peru and Bolivia, *Drepanocladus longifolius* (Figure 84) is another deep-water moss (Richards 1984). It is not as deep as the moss occurrences reported by Terneus (2001), but reaches depths to 29 m and dominates one of the submerged vegetation zones in the lake.



Figure 84. *Drepanocladus longifolius*, a deep-water moss in the Andes in Lake Titicaca. Photo by Juan David Parra, MBG, through Creative Commons.

Seepage Areas

Volk (1979) reported *Riccia cavernosa* (Figure 85) (a nitrophilous species), *R. runssorensis*, and *R. volkii* from seepage areas around dams in southwest Africa. Similarly, Pettet (1967) reported several species of *Riccia* from seepage areas in the Sudan. In addition, Pettet found *Tortula bogosica* (see Figure 86), *Barbula unguiculata* (Figure 87), *Physcomitrium niloticum* (Figure 88), *Funaria* (Figure 89), and *Bryum* (Figure 90) from such areas.



Figure 85. *Riccia cavernosa*, a species from seepage areas around dams in southwest Africa. Photo by Des Callaghan, with permission.



Figure 86. *Tortula hoppeana*; *Tortula bogosica* occurs in seepage areas in southwest Africa. Photo by Bryophyte CNPS, through Creative Commons.



Figure 87. *Barbula unguiculata*, a species of seepage areas in southwest Africa. Photo by Michael Lüth, with permission.



Figure 88. *Physcomitrium collenchymatum* from pond edge; *Physcomitrium niloticum* occurs in seepage areas of southwest Africa. Photo by Fred Essig, with permission.



Figure 89. *Funaria hygrometrica* with capsules, a species that occurs in seepage areas of southwest Africa. Photo by Li Zhang, with permission.



Figure 90. *Bryum pseudotriquetrum* by stream; species of *Bryum* occur in seepage areas in southwest Africa. Photo by Michael Lüth, with permission.

Xeric Habitats

Subtropical Israel provides us with a glimpse of the importance of climate, particularly water availability. Distribution of bryophytes there depends on climate, altitude, other vegetation, and shelter (Bischler 2002). Israel is one of the drier sites on the Mediterranean, and the low liverwort species richness reflects this fact. Within Israel, species richness of liverworts is lowest in the arid region and highest in the Mediterranean zone. Those liverworts that are able to grow in the arid zone are also able to grow under less severe conditions and have a wide geographic distribution, whereas many of the Mediterranean species are absent in the arid zone, but otherwise widely distributed. The flora of the country tends to be cosmopolitan and no endemics are known.

To succeed in habitats that have long dry periods interrupted by short periods of moisture, bryophytes must be able to recover quickly from desiccation. Di Nola *et al.* (1983) found that the **Pottiaceae** mosses *Tortula brevissima* (Figure 91) and *Trichostomopsis aaronis* (see Figure 92) are able to resume photosynthesis and respiration rapidly after prolonged desiccation.

Furthermore, they suffer little high light intensity damage. The chlorophyll is ready to resume photosynthesis without additional chlorophyll synthesis first. This is true for some temperate species as well, as seen in the Mediterranean moss *Didymodon fallax* (Figure 93), whereas *Homalothecium aureum* (Figure 94) has a slower recovery and is more sensitive to desiccation. But the temperate *Pohlia* (subgenus *Mniobryum*; Figure 95) sp. was unable to survive prolonged desiccation, exhibiting a lack of drought tolerance.



Figure 91. *Tortula brevissima* with capsules, a species that is able to resume photosynthesis and respiration rapidly after prolonged desiccation. Photo by Michael Lüth, with permission.



Figure 92. *Trichostomopsis umbrosa*; *Trichostomopsis aaronis* is a species that is able to resume photosynthesis and respiration rapidly after prolonged desiccation. Photo by Jan-Peter Frahm, with permission.



Figure 93. *Didymodon fallax*, a temperate species that is ready to resume photosynthesis without additional chlorophyll synthesis. Photo by Michael Lüth, with permission.



Figure 94. *Homalothecium aureum*, a temperate species with a slower recovery from desiccation and greater sensitivity to desiccation. Photo by Michael Lüth, with permission.



Figure 95. *Pohlia melanodon*; temperate species in this subgenus (*Mniobryum*) are unable to survive desiccation. Photo by Jan-Peter Frahm, with permission.

Frey (1986) noted the large percentage of endemic species in the arid parts of southwest Asia. Notable genera with endemic species include *Tortula* (Figure 86, Figure 91), *Crossidium* (Figure 122), and *Targionia* (Figure 102).

Pócs *et al.* (2007) reported on dry-land communities in Kenya. They described a community of *Mannia capensis* (Figure 96) that was accompanied by *Exormotheca pustulosa* (Figure 97), *Gongylanthus ericetorum* (Figure 98), *Plagiochasma rupestre* (Figure 99), *Riccia congoana* (Figure 100), *Riccia crinita* (Figure 101), and *Targionia hypophylla* (Figure 102), all liverworts. They identified several other associations in the dry lands. *Plagiochasma microcephalum* (see Figure 99) was accompanied by *Asterella* cf. *linearis* (see Figure 103), *Exormotheca pustulosa*, and *Riccia albolimbata* (Figure 104-Figure 105). *Riccia lanceolata* is widespread in tropical Africa, where it reaches a high diversity. This genus is particularly adapted to the seasonal rain, going dormant, then springing to growth when the rain arises. Other important *Riccia* species include *Riccia microciliata* (Figure 106), accompanied by *Riccia congoana*, *Riccia crinita*, and *Riccia okahandjana* (Figure 107). Widespread species include *Riccia congoana* and *Riccia atropurpurea* (Figure

108), accompanied by *Exormotheca pustulosa*, *Riccia crinita*, *Targionia hypophylla*.



Figure 96. *Mannia capensis*, a species forming a dry-land community in Kenya. Photo by Tony Benn, through Creative Commons.



Figure 97. *Exormotheca pustulosa*, a species in the *Mannia capensis* dry-land community in Kenya. Photo by Michael Lüth, with permission.



Figure 98. *Gongylanthus ericetorum*, a species in the *Mannia capensis* dry-land community in Kenya. Photo by Jan-Peter Frahm, with permission.



Figure 99. *Plagiochasma rupestre*, a species in the *Mannia capensis* dry-land community in Kenya. Photo by Alan Rockefeller, through Creative Commons.



Figure 102. *Targionia hypophylla*, a species of vertical volcanic cliffs in Kenya. Photo by Catherine Reeb, through Creative Commons.



Figure 100. *Riccia congoana*, a species in the *Mannia capensis* dry-land community in Kenya. Photo by Catherine Reeb, through Creative Commons.



Figure 103. *Asterella africana*; *Asterella cf. linearis* is a species in the *Mannia capensis* dry-land community in Kenya. Photo by Jonathan Sleath, with permission.



Figure 101. *Riccia crinita*, a species in the *Mannia capensis* dry-land community in Kenya. Photo by Štěpán Koval, with permission.

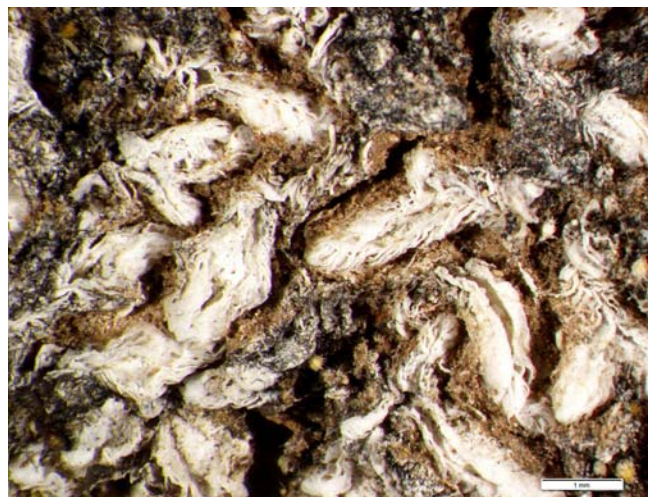


Figure 104. *Riccia albolimbata* dry, a species in the *Plagiochasma microcephalum* dry-land community in Kenya. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 105. *Riccia albolimbata* wet; the ability to rehydrate and resume growth permits this species to live in dry-land areas with seasonal rainfall in Kenya. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 106. *Riccia microciliata*, a species in the *Plagiochasma microcephalum* dry-land community in Kenya. Photo by Catherine Reeb, through Creative Commons.



Figure 107. *Riccia okahandjana*, an important *Riccia* species in the dry-land communities in Kenya. Photo by A. A. Dreyer, permission pending.



Figure 108. *Riccia atropurpurea* on sandstone, a widespread species in southwest Asia. Photo by Catherine Reeb, through Creative Commons.

Savannahs

In their study of savannah bryophytes in southwest Nigeria, Makinde and Odu (1994) found little bryophyte diversity. Liverworts were rare.

Oyesiku and Egunyomi (2001, 2002) have explored savannah bryophytes in southwestern Nigeria. They likewise found that mosses were far more common than liverworts in the dry savannah. The intense dryness is unfavorable to liverworts. Tree bark, however, provides some protection, permitting corticolous bryophytes to live in areas with bush burning. On the trees in relatively closed stands, bryophytes, particularly **mat**-forming species, are able to spread from the base to locations under 3 m height. Some of these bryophytes [*Hyophila* (Figure 109), *Erythrodontium* (Figure 110), *Riccia* (Figure 85)] are specialists at specific heights. Generalists with no height preference include the mosses *Fissidens* (Figure 51, Figure 67), *Calymperes* (Figure 11, Figure 30), *Thuidium* (Figure 111), and the leafy liverwort *Lejeunea* (Figure 47). Among these epiphytes, 60% of the mat species are dominant on host trees; the co-dominant tuft species comprise 34%.

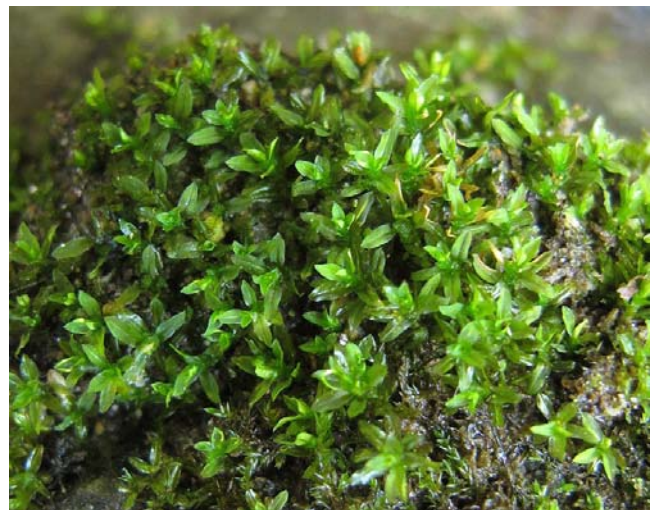


Figure 109. *Hyophila involuta*; members of this genus are specialists at specific heights in the savannahs. Photo by Michael Lüth, with permission.



Figure 110. *Erythrodontium squarrosus* from the Neotropics; members of this genus are specialists at specific heights in the savannahs. Photo by Michael Lüth, with permission.



Figure 113. *Sematophyllum subsimplex*, a savannah species in Corrado, Brazil. Photo by Yelitza Leon, through Creative Commons.



Figure 111. *Thuidium peruvianum* from the Neotropics; members of this genus are specialists at specific heights above ground in the savannahs. Photo by Michael Lüth, with permission.



Figure 114. *Sematophyllum subpinnatum*, a savannah moss in the Cerrado, Brazil. Photo by Michael Luth, with permission.

Silva Bonfim *et al.* (2018) collected bryophytes from a Cerrado fragment in Caxias, Maranhão, Brazil. This area is mostly savannah. They identified 175 bryophyte samples in 12 families (10 mosses, 2 liverworts), 17 genera (15 mosses, 2 liverworts), and 23 species (21 mosses, 2 liverworts). The **Sematophyllaceae** was best represented (*Trichosteleum subdemissum*, *Sematophyllum subsimplex* (Figure 113), *Sematophyllum subpinnatum* (Figure 114), and *Taxithelium planum* (Figure 115)). **Dicranaceae**, **Fissidentaceae** (Figure 51, Figure 67), and **Pottiaceae** (Figure 86-Figure 87, Figure 91-Figure 93) followed with three species each.



Figure 112. Cerrado savannah in Brazil. Photo by Conrado, through Creative Commons.



Figure 115. *Taxithelium planum*, a savannah moss in the Cerrado, Brazil. Photo by Scott Zona, with permission.

Succession

In their study of epiphytes in an Amazonian savannah in Brazil, Gottsberger and Morawetz (1993) noted that lichens and bryophytes have a successional relationship with their host trees. Young trees have lichen dominants. These lichens usually are diminished in older trees and bryophytes assume abundance, apparently supressing the lichens.

Life Cycle Strategies

Makinde and Odu (1994) followed the reproductive cycles of four species [*Archidium ohioense* (Figure 116), *Bryum coronatum* (Figure 117), *Fissidens minutifolius* (see Figure 51, Figure 67), *Trachycarpidium tisserantii*] that reproduce predominately sexually. They found that the protonemata and gametophytes are produced in the field in March-April. Capsule dehiscence and spore dispersal occurs in September-October. The development of gametangia through the completion of dispersal all occur within the rainy season. **Cleistocarpous capsules** (capsules with no operculum and that open irregularly) of *A. ohioense* and *T. tisserantii* do not disperse their spores easily. All species experience only a short period between the formation of sex organs and the dehiscence of the capsule.



Figure 116. *Archidium ohioense*, a species with cleistocarpous capsules and a short period between fertilization and ripe capsules. Photo by Li Zhang, with permission.

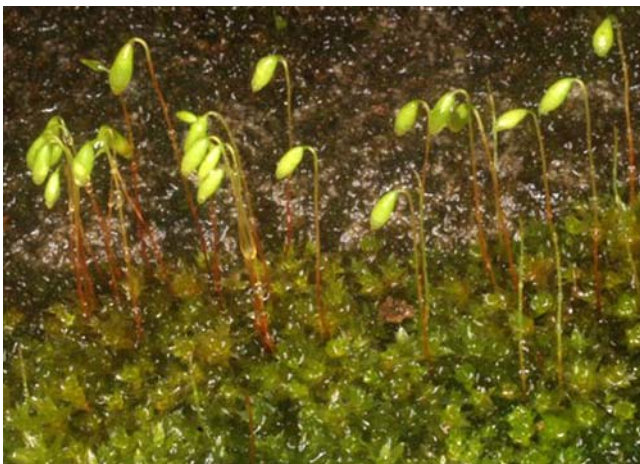


Figure 117. *Bryum coronatum*; in the Nigerian savannah, development of gametangia through the completion of dispersal all occur within the rainy season in this species. Photo by Jan-Peter Frahm, with permission.

When long periods of drought are a regular part of the environment, reproduction can be challenging. Spore longevity would help to solve this problem. However, when Egunyomi (1979) tested spore viability of 20 tropical moss species, only 7 germinated after more than two years of storage, and only 4 species had as much as 50%

germination. Freezing for 1 week or more was detrimental to all 20 species. *Microcampylopus nanus* (see Figure 118) had the highest spore longevity and germination after desiccation. Other species that survived desiccation for at least two years were *Weissia papillosa* (see Figure 119), *Mittenothamnium overlaetii* (Figure 120), and *Weisiopsis nigeriana*. What is interesting is that these four species are from a locality that is persistently wet.



Figure 118. *Microcampylopus laevigatus*; *Microcampylopus nanus* has high spore longevity and germination after desiccation. Photo by Jan-Peter Frahm, with permission.



Figure 119. *Weissia multicapsularis*; *Weissia papillosa* survives desiccation for at least two years. Photo by David T. Holyoak, with permission.



Figure 120. *Mittenothamnium reptans*; *Mittenothamnium overlaetii* can survive desiccation for at least two years. Photo by Michael Lüth, with permission.

Although we cannot rule out spore longevity, we need to find other means to explain reproductive success in these dry-habitat mosses. During and coworkers (During 1998, 2007; During & Moyo 1999) examined the diaspore bank in a savannah in Zimbabwe. They determined at least 2 hornworts, 10 liverworts, and 22 mosses that emerge from these soil samples. Some of these were in large numbers. Some of these species, such as *Micromitrium tenerum* (Figure 121), were rare or previously unknown in Africa or Zimbabwe. An added advantage for these diaspores is that they are able to survive above-ground burning.



Figure 121. *Micromitrium tenerum*, a species that can survive desiccation for at least two years. Photo by Jan-Peter Frahm, with permission.

Tropical Deserts

Deserts are not very friendly to bryophytes, and this habitat is likewise unfriendly for bryologists. Tropical deserts are often among the worst of these due to their even higher temperatures. Hence, systematic studies of bryophytes in these habitats are rare. Nevertheless, the guileless bryophytes and their adventurous observers can occur in these inhospitable places.

O'Shea (1997) reported over 3000 taxa of mosses in sub-Saharan Africa. Of these, 77% were considered endemic at the time. Because of the small number of bryologists exploring the vast area of Africa, it may still be a long time before we understand the African flora well enough to know how many of these are truly endemic.

The moss *Crossidium laevipilum* (Figure 122) occurs in semidesert conditions in Kenya, where it is associated with many xeric species (Pócs *et al.* 2007). *Didymodon revolutus* (Figure 123) occurs on vertical volcanic cliffs. This species has both axillary and rhizoidal gemmae, contrasting with American plants that are only known to have axillary gemmae. This species is known as a xerophyte in the desert and semidesert of southern United States, Mexico, Guatemala, and Ecuador.



Figure 122. *Crossidium laevipilum*, a species of semi-desert conditions in Kenya. Photo by Michael Lüth, with permission.

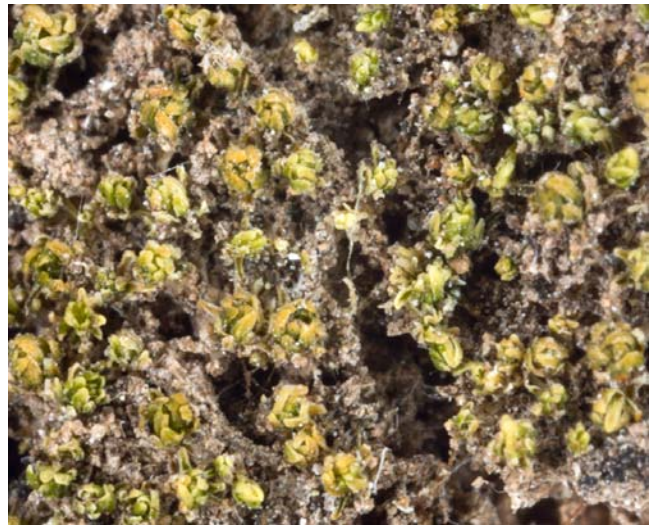


Figure 123. *Didymodon revolutus* dry, a species of vertical volcanic cliffs in Kenya. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

At the edge of the Tunisian Sahara, Pócs (2007) found the community of *Crossidium laevipilum* (Figure 122)-*Tortula atrovirens* (Figure 124) to be dominant. Only the tips of the plants and apical hair points, if present, extended above the sand. The hair points can protect against UV light and collect moisture. Most of the bryophytes, like these two, are in the *Pottiaceae*. The rock cliffs can support a community dominated by *Grimmia capillata* (Figure 125)-*Tortula revolvens* (Figure 126). The association of *Eucladium verticillatum* (Figure 127-Figure 128) and *Didymodon tophaceus* (Figure 129) occurs only near waterfalls of the Tamerza oasis. North-facing cliff bases provide enough shelter to support *Bryum funckii* (Figure 130)-*Didymodon australasiae* (Figure 131) associations. On the exposed limestone gravel scree and loess cliffs one can find the pioneer community of *Crossidium squamiferum* (Figure 132) and *Aloina bifrons* (Figure 133). The northern part is less extreme in climatic conditions and one can find the *Didymodon australasiae*-*Tortula revolvens* community.



Figure 124. *Tortula atrovirens*, part of the dominant *Crossidium laevipilum-Tortula atrovirens* community at the edge of the Tunisian Sahara. Photo by John Game, through Creative Commons.



Figure 127. *Eucladium verticillatum*, part of the waterfall association of *Eucladium verticillatum* and *Didymodon tophaceus* at the edge of the Tunisian Sahara. Photo by Michael Lüth, with permission.



Figure 125. *Grimmia capillata* with capsules, dry – part of the *Grimmia capillata-Tortula revolvens* association on rock cliffs at the edge of the Tunisian Sahara. Photo by Hank Greven, with permission.



Figure 128. *Eucladium verticillatum*, showing individual plants. Photo by Hermann Schachner, through Creative Commons.

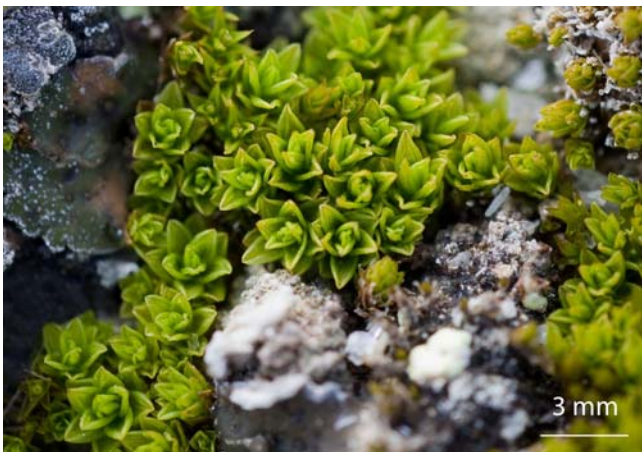


Figure 126. *Tortula revolvens* – part of the *Grimmia capillata-Tortula revolvens* association on rock cliffs at the edge of the Tunisian Sahara. Photo from Proyecto Musgo, through Creative Commons.



Figure 129. *Didymodon tophaceus* with capsules, part of the waterfall association of *Eucladium verticillatum* and *Didymodon tophaceus* at the edge of the Tunisian Sahara. Photo by David T. Holyoak, with permission



Figure 130. *Bryum funckii*, a species of the *Bryum funckii*-*Didymodon australasiae* association on north-facing cliff bases that provide enough shelter for them to survive at the edge of the Tunisian Sahara. Photo by Michael Lüth, with permission.



Figure 131. *Didymodon australasiae*, a species of the *Bryum funckii*-*Didymodon australasiae* association on north-facing cliff bases that provide enough shelter for their survival at the edge of the Tunisian Sahara. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.



Figure 132. *Crossidium squamiferum*, a member of the *Crossidium squamiferum* and *Aloina bifrons* association – a pioneer community on the exposed limestone gravel scree and loess cliffs at the edge of the Tunisian Sahara. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.



Figure 133. *Aloina bifrons* with capsules, a member of the *Crossidium squamiferum* and *Aloina bifrons* association – a pioneer community on the exposed limestone gravel scree and loess cliffs at the edge of the Tunisian Sahara. Photo by Ben Carter, through Creative Commons.



Figure 134. *Aloina bifrons*, showing the thickened leaves that are able to maintain water and hair points that collect water. Photo by Martin Hutten, with permission.

The thallose liverworts in such dry areas are "tiny" and become practically invisible during the dry season, reappearing when the rains arrive. This ability is particularly common in the **Ricciaceae** (Pócs *et al.* 2007). The *Riccia* species (Figure 100-Figure 101, Figure 104-Figure 106) in these dry habitats exhibit 20% endemism while another 20% are widespread, often cosmopolitan xerophytes. Most of the mosses are in the **Pottiaceae** (Figure 122-Figure 123). These xerophytic mosses have crispate, often contorted leaves with inrolled or recurved margins (Kürschner 2004).

Kürschner (2000) described the bryophyte flora of the Arabian Peninsula (Figure 135) and Socotra (Figure 136), much of which is desert. Prior to 1980, no bryophytes were known from the entire peninsula. The bryological flora is characteristic for the monsoon-influenced peninsula, including 1 hornwort, 50 liverworts, and 173 mosses, with many Palaeotropical and Afro-montane taxa. On the other hand, the arid and semi-arid regions, with winter rainfall, are dominated by species that are drought adapted and drought tolerant. These include many **Pottiaceae** and thalloid liverworts that go dormant during the drought.



Figure 135. Arabian Peninsula desert and oasis in Oman. Photo by Hendrik Dacquin aka loufi, through Creative Commons.



Figure 137. *Mannia androgyna*, a member of the *Mannia androgyna-Barbula unguiculata* alliance; the *Riccietum jovet-astii-argenteolimbatae* association is in this alliance. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.



Figure 136. Desert community of Dixam canyon, Socotra. Photo by Gerry and Bonni, through Creative Commons.

Later, Kürschner (2003) conducted a phytosociological analysis of the *Riccietum jovet-astii-argenteolimbatae* association as a new association found in the Jabal Arays area of Yemen. This association consists predominantly of *Riccia jovet-astiae* and *Riccia cf. albolimbata* (Figure 104-Figure 105). Kürschner identified this association as being grouped within the alliance of *Mannia androgyna* (Figure 137) with *Barbula unguiculata* (Figure 87). The new association typically occurs on shallow soils that overly volcanic rock outcrops, where it occurs in the understory of *Sterculia africana arabica* (Figure 138) woodland in monsoon-affected areas. The life strategy here is that of a shuttle species with large spores. Thus dispersal is short range. Spores in a diaspore bank help to maintain the presence of these liverworts. Of minor importance is their colonist strategy and they live on the soil where they can go dormant until monsoon season.



Figure 138. *Sterculia africana*, a species that occurs on shallow soils that overly volcanic rock outcrops in monsoon-affected areas of Yemen. Photo by Peter B. Phillipson, through Creative Commons.

Summary

Neotropical floodplains include the **igapó** and **várzea** habitats, seasonally inundated, and supporting different bryophyte communities. Sexual reproduction predominates among the bryophytes. The leafy liverwort family **Lejeuneaceae** predominates in species richness, while the family **Calymperaceae** has the most moss species.

Mangrove forests are limited in bryophyte species because of saltwater. Nevertheless, **Calymperaceae** are among the few moss species present, with **Lejeuneaceae** being the most species-rich among the liverworts. Bryophytes in these floodplains are passive accumulators of nutrients and help to retain them within the floodplain.

Tropical peatlands are effectively restricted to higher altitudes and include some of the well-known high latitude species such as *Sphagnum magellanicum* and *S. recurvum*. *Sphagnum platyphyllum* is common in peatlands rich in iron. Two mire types are dominated by tracheophytes, with the moss *Campylopus reflexisetus* occurring on the cushions. Two are dominated by bryophytes, differing in vegetation with differences in conductivity and nutrients. Genetic variation within species may be highly variable, as seen in *Sphagnum tumidulum* from Reunion Island. At least some *Sphagnum* spores have greater longevity in the absence of oxygen, permitting them to survive in the peat.

Few tropical bryophytes live permanently submerged except at high elevations. In low elevations, high temperatures, low CO₂ levels, and low light intensities result in negative carbon gain. But in the Andes, several rare species are associated with torrential waters.

In **rheophytic** habitats, one can find leafy liverworts in the **Lejeuneaceae**, with a number of moss species on rheophytic shrubs, roots, and rocks where they are seasonally submerged. The absence of tropical studies on rheophytes leaves species awaiting discovery. Nevertheless, a number of families with rheophytic representatives are known.

Glacial lakes may have such species as *Herbertus sendtneri*. These lakes and other high-altitude tropical lakes are isolated by the hot valleys that are unsuitable as vegetative dispersal avenues for bryophytes.

Seepage areas often have species of *Riccia* and mosses that are typical of disturbed areas such as *Barbula unguiculata*, *Funaria*, and *Bryum*.

The tropics create a number of xeric habitats. These have low liverwort diversity but are able to support desiccation-tolerant mosses, particularly members of the **Pottiaceae**. These mosses are able to resume photosynthesis quickly upon rewetting. Among the liverworts, *Riccia* species can become dormant for prolonged periods of time, then expand and resume growth. Among these xeric habitats are savannahs, where liverworts are rare and little diversity is common. Nevertheless, the liverworts *Riccia* and **Lejeuneaceae** can occur as epiphytes. The meager evidence on life cycle strategies suggests that the sexual cycle takes advantage of the short wet periods, with spore dispersal

likewise occurring in wet periods. Some mosses have **cleistocarpous** capsules. Spores in 20 tested species exhibit limited longevity. However, spores seem to survive better in diaspore banks. Deserts, as might be expected, have their highest bryophyte diversity in the **Pottiaceae** and **Ricciaceae**. Canyon and shaded cliffs have a higher diversity.

Acknowledgments

Thank you to Tatiany Oliveira da Silva for her contributions of papers, images, and comments. Her helpful discussions kept me going on this part of the world I know so little about and clarified some of the terminology of the inundated forests. Thank you to Claudine Ah-Peng for helping me obtain an image of *Sphagnum tumidulum*. And my appreciation to all the photographers who have put their images in Creative Commons.

Literature Cited

- Akiyama, H. 1992a. Rheophytes of bryophytes in wet tropics of Southeastern Asia. *Nat. Environ. Sci. Res.* 5: 43-55.
- Akiyama, H. 1992b. Morphological and ecological aspects of moss rheophytes. *Plant Morph.* 4: 23-28. [in Japanese] <https://doi.org/10.5685/plmorphol.4.23>
- Bartlett, J. K. and Vitt, D. H. 1986. A survey of the species in the genus *Blindia* (Bryopsida, Seligeriaceae). *N. Z. J. Bot.* 24: 203-246.
- Bednarek-Ochyra, H. 2015. *Bucklandiella lamprocarpa* (Musci, Grimmiaceae) in the central and northern Andes. *Cryptog. Bryol.* 36: 81-90.
- Benavides, J. C., Vitt, D. H., and Wieder, R. K. 2013. The influence of climate change on recent peat accumulation patterns of *Distichia muscoides* cushion bogs in the high-elevation tropical Andes of Colombia. *J. Geophys. Res. Biogeosci.* 118: 1627-1635.
- Bischler, H. 2002. Species-environment relationships and diversity of liverworts in Israel. *Israel J. Plant Sci.* 50(suppl.): 15-23.
- Bosnian, A. F., Molen, P. C. van der, Young, R., and Cleef, A. M. 1993. Ecology of a paramo cushion mire. *J. Veg. Sci.* 4: 633-640.
- Cerqueira, G. R., Ilkiu-Borges, A. L., and Ferreira, L. V. 2016. Seasonality of reproduction of epiphytic bryophytes in flooded forests from the Caxiuanã National Forest, Eastern Amazon. *An. Acad. Brasil. Ciên.* 88: 903-910.
- Cerqueira, G. R., Ilkiu-Borges, A. L., and Ferreira, L. V. 2017. Species richness and composition of epiphytic bryophytes in flooded forests of Caxiuanã National Forest, Eastern Amazon, Brazil. *An. Acad. Brasil. Ciên.* 89. available at <http://www.scielo.br/scielo.php?pid=S0001-37652017005023105&script=sci_arttext>.
- Churchill, S. P. 2016. Bryophyta. In: Bernal, R., Gradstein, S. R., and Celis, M. (eds.). *Catálogo de plantas y líquenes de Colombia*. Universidad Nacional de Colombia, Bogotá, pp. 353-442.
- Churchill, S. P. 2018. *Herbertus sendtneri*. <<http://www.tropicos.org/Name/35208495?tab=specimens>>.
- Cleef, A. M. 1981. The vegetation of the paramos of the Colombian Cordillera Oriental. In: Hammen, T. van der.

- (ed.). The Quaternary of Colombia, Vol. 9. Elsevier, Amsterdam.
- Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., and Longino, J. T. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322: 258-261.
- Crandall-Stotler, B. J. and Gradstein, S. R. 2017. A new riverine species of the genus *Fossombronia* (Pelliales, Fossombroniaceae) from Ecuador. *Bryo. Divers. Evol.* 39: 94-101.
- Cuatrecasas, J. 1968. Páramo vegetation and its life forms, in geo-ecology of the mountainous regions of the tropical Americas. Troll, C. (ed.). Proceedings of the UNESCO Mexico Symposium. Dümmlers Verlag, Bonn, Germany, pp. 163-186.
- Di Nola, L., Mayer, A. M., and Heyn, C. C. 1983. Respiration, photosynthesis and drought tolerance in mosses from various habitats in Israel. *Israel J. Bot.* 32: 189-202.
- During, H. J. 1998. De diasporeenvoorraad in de bodem van een savanne in Zimbabwe. [The diaspore bank in the bottom of a savannah in Zimbabwe.]. *Bauxbaumiella* 45: 12-13.
- During, H. J. 2007. Episodic bryophytes in the diaspore bank of a Zimbabwean savanna. *Lindbergia* 32: 55-61.
- Edwards, S. R. 1980. A revision of West Tropical African Calymperaceae I. *J. Bryol.* 11: 49-93.
- During, H. J. and Moyo, C. 1999. The diaspore bank of bryophytes in a Zimbabwean savanna. *Haussknecht. Beih. (Ricleft Grolle-Festschrift)* 9: 111-114.
- Eddy, A. 1977. Sphagnales of Tropical Asia. *Bull. Brit. Mus. Nat. Hist. Bot.* 5: 359-445.
- Eddy, A. 1988. A Handbook in Malesian Mosses. Vol. I, Sphagnales to Dicranales. Natural History Museum Publication, London.
- Eddy, A. 1990. A Handbook of Malesian Mosses. Vol. 2, Leucobryaceae to Buxbaumiaceae. Natural History Museum Publication, London.
- Eddy, A. 1996. A Handbook of Malesian Mosses. Vol. 3, Splachnobryaceae to Leptostomataceae. Natural History Museum Publication, London.
- Egunyomi, A. 1979. The viability of spores of some tropical moss species after longtime storage and their survival chances in nature. *J. Hattori Bot. Lab.* 45: 167-171.
- Feng, L., Sundberg, S., Ooi, M. K. J., Wu, Y.-H., Wang, M., and Bu, Z.-J. 2018. Oxygen-deficiency and allelochemicals affect *Sphagnum* spore persistence in peatlands. *Plant Soil.* 432: 403-413.
- Ferreira, L. V., Almeida, S. S., Amaral, D. D., and Parolin, P. 2005. Riqueza e Composição de Espécies da Floresta de Igapó e Várzea da Estação Científica Ferreira Penna: Subsídios para o Plano de Manejo da Floresta Nacional de Caxiuanã. *Botânica* 56: 103-116.
- Ferreira, L. V., Chaves, P. P., Cunha, D. A., Matos, D. C. L., and Parolin, P. 2013. Variação da Riqueza e Composição de Espécies da Comunidade de Plantas entre as florestas de Igapós e Várzeas na Estação Científica Ferreira Penna-Caxiuanã na Amazônia Oriental. [Variation of the wealth and composition of species of the plant community between the forests of igapós and várzeas at the Ferreira Penna-Caxiuanã Scientific Station in the Eastern Amazon.]. *Botânica* 64: 175-195.
- Frangi, J. L. and Lugo, A. E. 1992. Biomass and nutrient accumulation in ten year old bryophyte communities inside a flood plain in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 24: 106-112.
- Fritz, C., Pancotto, V. A., Elzenga, J. T. M., Visser, E. J. W., Grootjans, A. P., Pol, A., Iturraspe, R., Roelofs, J. G. M., and Smolders, A. J. P. 2011. Zero methane emission bogs: Extreme rhizosphere oxygenation by cushion plants in Patagonia. *New Phytol.* 190: 398-408.
- Gates, F. C. 1915. A *Sphagnum* bog in the tropics. *J. Ecol.* 3: 24-30.
- Gottsberger, G. and Morawetz, W. 1993. Development and distribution of the epiphytic flora in an Amazonian savanna in Brazil. *Flora* 188: 145-151.
- Gradstein, S. R. and Benitez, A. 2014. A second locality for the critically endangered *Colura irrorata* (Lejeuneaceae) in the Ecuadorian Andes. *J. Bryol.* 36: 151-155.
- Gradstein, S. R. and Reiner-Drehwald, M. E. 2007. On the status of *Neopotamojeunea* E. Reiner (Lejeuneaceae), with description of a new species. *Syst. Bot.* 32: 487-492.
- Gradstein, S. R. and Váña, J. 1999. On the taxonomy of *Kymatocalyx* and *Stenorhipis* (Cephalozellaceae). *Haussknechtia Beih.* 9: 155-170.
- Gradstein, S. R., Churchill, S. P., and Salazar Allen, N. 2001a. Guide to the Bryophytes of Tropical America. *Mem. N. Y. Bot. Gard.* 86: 1-577.
- Gradstein, S. R., Griffin, D. III, Morales, M. I., and Nadkarni, N. M. 2001b. Diversity and habitat differentiation of mosses and liverworts in the cloud forest of Monteverde, Costa Rica. *Caldasia* 23: 203-212.
- Gradstein, S. R., Reiner-Drehwald, M. E., and Jost, L. 2004. The systematic position and distribution of *Myriocolea irrorata* (Lejeuneaceae, Hepaticae), an endangered liverwort from the Ecuadorian Andes. *J. Hattori Bot. Lab.* 93: 235-248.
- Gradstein, S. R., Ilkiu-Borges, A.-L., and Vanderpoorten, A. 2011. Habitat specialization triggers the evolution of unusual morphologies: The case of *Cololejeunea stotleriana* sp. nov. from Ecuador. *Bryologist* 114: 9-22.
- Gradstein, R., Vanderpoorten, A., Reenen, G. van, and Cleef, A. 2018. Mass occurrence of the liverwort *Herbertus sendtneri* in a glacial lake in the Andes of Colombia. *Rev. Acad. Colomb. Cien. Exact. Fisic. Nat.* 42: 221-229.
- Griffin, D., Gradstein, S. R., Aguirre, J. 1982. On a new antipodal element in the Neotropical paramos: *Dendrocryphaea latifolia* sp. nov. *Acta Bot. Neerl.* 31: 175-184.
- Hedenäs, L. 2003. Amblystegiaceae. *Flora Neotrop. Monogr.* 89: 1-107.
- Kleinebecker, T., Hölzel, N., and Vogel, A. 2010. Patterns and gradients of diversity in South Patagonian ombrotrophic peat bogs. *Austral. Ecol.* 35(1): 1-12.
- Koponen, T. and Norris, D. H. 1983. Bryophyte flora of the Huon Peninsula, Papua New Guinea. I. Study area and its bryological exploration. *Ann. Bot. Fennici* 20: 15-29.
- Kürschner, H. 2000. Bryophyte flora of the Arabian Peninsula and Socotra. *Bryophytorum Bibliotheca* 55: 131 pp, 17 figs, 224 maps. *Rev. in Nova Hedw.* 71: 267.
- Kürschner, H. 2003. The Riccietum jovet-astii-argenteolimbatae ass. nov. of the Jabal Arays area, Yemen-life strategies of a remarkable xerotropical African bryophyte community. *Nova Hedw.* 76: 399-413.
- Kürschner, H. 2004. Life strategies and adaptations in bryophytes from the Near and Middle East. *Turk. J. Bot.* 28: 73-84.
- Liu, Y., Ah-Peng, C., Wilding, N., Bardat, J., Devos, N., Carter, B., and Shaw, A. J. 2014. Population structure in the tropical peatmoss, *Sphagnum tumidulum* Besch. (Sphagnaceae). *Bryologist* 117: 329-335.

- Lopes, M. O., Pietrobon, M. R., Carmo, D. M., and Peralta, D. F. 2016. Comparative study of communities of bryophytes in different degrees of flooding in the municipality of São Domingos do Capim, Pará State, Brazil. *Hoehnea* 43: 159-171.
- Ma, W.-Z., Shevock, J. R., and Enroth, J. 2014. Rediscovery of the monospecific genus *Cyrtodontopsis* (Cryphaeaceae) in China: A species restricted to flood plain habitats. *Acta Bryolichenol. Asiatica* 5: 141-149.
- Mägdefrau, K. 1973. *Hydropogon fontinaloides* (Hook.) Brid., ein periodisch hydro-aerophytisches Laubmoos des Orinoco und Amazonas. *Herzogia* 3: 141-149.
- Makinde, A. M. and Odu, E. A. 1994. Phenological studies of selected savanna mosses of south-western Nigeria. *Experientia* 50: 616-619.
- McQueen, B. C. 1991. Niche breadth and overlap of four species of *Sphagnum* in southern Ecuador. *Bryologist* 94: 39-43.
- McQueen, C. B. 1995. Niche breadth and overlap of *Sphagnum* species in Costa Rica. *Trop. Bryol.* 11: 119-128.
- McQueen, C. B. 1997. Niche diversification of *Sphagnum* in Bolivia. *Trop. Bryol.* 13: 65-74.
- Ochyra, R., Schmidt, C., and Bültmann, H. 1998. *Gradsteinia torrenticola*, a new aquatic moss species from Tenerife. *J. Bryol.* 20: 403-409.
- Ochyra, R. & H. Bednarek-Ochyra. 1999. *Platyhypnidium grolleanum* (Musci: Brachytheciaceae), a new species from the Sudetes (Central Europe). *Haussknechtia Beih.* 9: 259-264.
- O'Shea, B. J. 1997. The mosses of sub-Saharan Africa 2. Endemism and biodiversity. *Trop. Bryol.* 13: 75-86.
- Oyesiku, O. O. and Egunyomi, A. 2001. Savanna bryophytes from the upper Ogun, south-western Nigeria. *J. Bryol.* 23: 67-70.
- Oyesiku, O. O. and Egunyomi, A. 2002. Vertical distribution and zone preference of bryophyte species on trees in savanna Southwestern Nigeria. *J. Sci. Technol. Res.* 1: 87-92.
- Pettet, A. 1967. Bryophytes of the Sudan. I. Khartoum Province. *J. Trans. Brit. Bryol. Soc.* 5: 316-331.
- Piedade, M. T. F., Parolin, P., and Junk, W. J. 2006. Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian black water floodplains. *Rev. Biol. Trop.* 54: 1171-1178.
- Pires, J. M. and Prance, G. T. 1985. The vegetation types of the Brazilian Amazon. Chapt. 7. In: Prance, G. T. and Lovejoy, E. T. *Key Environments: Amazonia*. Pergamon Press, Oxford, pp. 109-145.
- Pócs, T. 2007. Bryophyte communities at the communities at the edge of Tunisian Sahara, with the description of *Gymnostomum viridulum* Brid. subsp. *saharae*, subsp. nov. (Pottiaceae, Bryophyta). *Beih. Nova Hedw.* 131: 101-120.
- Pócs, T., Pócs, S., Chuah-Petiot, M. S., Malombe, I., and Masinde, S. 2007. East African bryophytes, XXIV. Records from the dry lands of Kenya, with a description of *Didymodon revolutus* var. nov. *africanus* (Pottiaceae). *Lindbergia* 32: 33-39.
- Piedade, M. T. F., Junk, W. J., Adis, J., and Parolin, P. 2005. Ecologia, Zonação e Colonização da Vegetação Arbórea das Ilhas Anavilhanas. [Ecology, zonation and colonization of Anavilhanas arboreal vegetation.]. *Pesquisas, Botânica* 56: 117-144.
- Piedade, M. T., Parolin, P., and Junk, W. J. 2006. Phenology, fruit production and seed dispersal of *Astrocaryum jauari* (Arecaceae) in Amazonian black water floodplains. *Rev. Biol. Trop.* 54: 1171-1178.
- Prance, G. T. 1980. A terminologia dos tipos de florestas amazônicas sujeitas a inundação. *Acta Amazon.* 10: 495-504.
- Rankin, A. H., Pressel, S., Duckett, J., Rimington, W. H., Hawes, I., Sumners, D. Y., Mackey, T. J., Castendyke, D., Schneider, H., and Jungblut, A. D. 2017. Characterisation of a deep-water moss from the perennially ice-covered Lake Vanda, Antarctica. *Polar Biol.* 40: 2063-2076.
- Reiner-Drehwald, E. 1999. On *Potamolejeunea polyantha* (Mont.) E. Reiner & Goda comb. nov. (Lejeuneaceae), a poorly known rheophytic liverwort from South America. *Haussknechtia Beih.* 9: 299-306.
- Richards, P. W. 1984. *Sciaromium lacustre* Herzog & Richards, sp. nov., a deep-water moss from Lake Titicaca (South America), with notes on its ecology. *J. Bryol.* 13: 33-38.
- Ruiz, D., Moreno, H. A., Gutierrez, M. E., and Zapata, P. A. 2008. Changing climate and endangered high mountain ecosystems in Colombia. *Sci. Tot. Environ.* 398: 122-132.
- Shevock, J. R., Ochyra, R., He, S., and Long, D. G. 2011. *Yunnanobryon*, a new rheophytic moss genus from southwest China. *Bryologist* 114: 194-203.
- Shevock, J. R., Ma, W. Z., and Akiyama, H. 2017. Diversity of the rheophytic condition in bryophytes: Field observations from multiple continents. *Bryo. Divers. Evol.* 39: 75-93.
- Silva Bonfim, M. A. da, Oliveira, R. F., Oliveira, R. R., Silva Gomes, G. da, Fátima Veras, M. de, Silva, M. L. A. da, Melo Nascimento, J. de, Silva, G. S. da, Santos-Silva, D. L. dos, Gaspar, J. C., Sousa, D. H. S. de, Silva, A. M., Martins, P. R. P., and Conceição, G. M. da. 2018. Bryophytes in Maranhão/Brazil: A New Area, a New Species List. Available from: https://www.researchgate.net/publication/335288454_Bryophytes_in_MaranhaoBrazil_A_New_Area_a_New_Species_List [accessed Aug 30 2019].
- Terneus, E. 2001. Aquatic plant communities of the páramo lakes of Volcán Chiles, Ecuador. In: Ramsay, P. M. (ed.). *The Ecology of Volcán Chiles: High-altitude Ecosystems of the Ecuador-Colombia Border*. Pebble & Shell, Plymouth, pp. 55-63.
- Thaitong, O. 1984. Bryophytes of the mangrove forest. *J. Hattori Bot. Lab.* 56: 85-87.
- Volk, O. H. 1979. Beiträge zur Kenntnis der Lebermoose (Marchantiales) aus Südwestafrika (Namibia) I. [Contributions to the knowledge of the liverworts (Marchantiales) from southwest Africa (Namibia) I.]. *Mitt Bot Staats. Münch* 15: 223-242.
- Whitaker, D. L. and Edwards, J. 2010. *Sphagnum* moss disperses spores with vortex rings. *Science* 329: 406-406.
- Wilding, N., Hedderson, T., Ah-Peng, C., and Magombo, I. 2016. Bryophytes of Kenya's Coastal Forests. A Guide to the Common Species. Published by authors in electronic format, 66 pp.
- Windolf, J. 1989. Bryophytes in a subtropical mangrove community. *Austrobaileya* 3: 103-107.
- Winton, M. D. de and Beever, J. E. 2004. Deep-water bryophyte records from New Zealand lakes. *N. Z. J. Marine Freshwat. Res* 38: 329-340.
- Wolfe, J. and McQueen, C. B. 1992. Biogeochemical ecology of six species of *Sphagnum* in Costa Rica. *Trop. Bryol.* 5: 73-78.
- Yamaguchi, T., Nakagoshi, N., and Nehira, K. 1987. Terrestrial bryophytes in mangrove forests in Japan. *Proc. Bryol. Soc. Japan* 4: 137-140.

CHAPTER 8-12

TROPICS: ROCKS AND INSELBERGS

JANICE M. GLIME AND TATIANY OLIVEIRA DA SILVA

TABLE OF CONTENTS

Adaptations	8-12-5
Life Cycle Strategies	8-12-5
Dispersal	8-12-8
Desiccation Recovery	8-12-9
Interactions with Other Plants.....	8-12-10
Lava Flows.....	8-12-11
Richness and Diversity	8-12-11
Africa	8-12-12
Neotropics.....	8-12-16
Summary.....	8-12-22
Acknowledgments	8-12-22
Literature Cited.....	8-12-22

CHAPTER 8-12

TROPICS: ROCK OUTCROPS AND INSELBERGS

JANICE M. GLIME AND TATIANY OLIVEIRA DA SILVA



Figure 1. Inselbergs in Mozambique, Africa. Photo by Ton Rulkens, through Creative Commons.

Rock outcrops and inselbergs provide unique habitats, usually being more xeric than surrounding habitats. An **inselberg** (Figure 1) is distinguished as "those isolated rock outcrops that stand out abruptly from surrounding plains" (Potembski & Barthlott 2012). The term appears to have been introduced by Bornhardt (1900). Both outcrops and inselbergs can differ in rock types, and this can promote different vegetation groupings. Potembski and Barthlott noted that study of the widespread granite inselbergs has been neglected, yet it is "remarkably" rich in plant life. Porembski (2007) identified the three hot spots of inselberg plant diversity on a global scale as southeastern Brazil, Madagascar, and southwestern Australia; the first two of these are tropical.

Barthlott *et al.* (1993) note that the flora of the inselbergs differs almost completely from that of the surrounding area, behaving like islands. They concluded

that the bare rock is covered almost completely by **Cyanobacteria** in French Guyana, but by lichens in the Ivory Coast. Nevertheless, the life forms are similar in the Palaeotropics and Neotropics. It would be interesting to make these same comparisons for bryophytes.

It is interesting that tracheophytes in such dry habitats may mimic some of the traits of bryophytes. These adaptations include forming **mats** and **poikilochlorophyllous** (lose chlorophyll and cease photosynthesis and transpiration when dry) behavior (Porembski & Barthlott 2000). It is incredible that of the approximately 330 species (in only 13 families) of tracheophytes that are desiccation-tolerant, close to 90% occur on inselbergs.

In Brazil, ironstone rock outcrops provide an adverse environment where daily temperatures vary widely, UV exposure is elevated, constant winds are present, and soils

are impermeable and have low water retention with high levels of iron (Peñaloza-Bojacá *et al.* 2018b). Such conditions favor a very rich and endemic community where xerophilic plants thrive.

Rock outcrops are not just bare rock, even in their earliest stages. These topographic differences include shallow depressions that can fill with water (Figure 2), drainage channels (Figure 3), vertical faces with directional N-S exposures (Figure 4), and horizontal plains (Figure 5). In Guinea, mats of *Afrotrilepis pilosa* (Figure 6) create protected habitats, habitats with extremes (*e.g.* Figure 5) that support ephemeral plants, and areas experiencing flushes that have their own distinct vegetation (Porembski *et al.* 1994). Sandstone outcrops of Fouta Djallon in Guinea (Figure 7) are species-rich and have a large number of endemics. Porembski and coworkers suggested this may be due to the combination of vertical differentiation, large area, long-term climate stability, and isolation. The granite inselbergs and **ferricretres** (hard, erosion-resistant layer of sedimentary rock, usually conglomerate or breccia, cemented into a duricrust by iron oxides), on the other hand, lack local endemics and have a lower species richness. The greatest diversity of inselberg vegetation of tropical Africa seems to occur in Tanzania, Malawi, Mozambique, Zambia, Zimbabwe, and Angola.



Figure 4. Colonizing plants on vertical surface of rock outcrop at Pedra do Cachorro, northeast Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 2. Rock outcrop at Pico do Papagaio, Brazil, showing shallow pool in rock in the foreground. Photo courtesy of Tatiany Oliveira da Silva.



Figure 5. Fully exposed horizontal rock outcrop at Pedra, Brazil. This dark-colored rock is even more formidable because it absorbs heat. Photo courtesy of Tatiany Oliveira da Silva.



Figure 3. Rock outcrop, Pedra da Massa, Brazil, showing drainage channels descending from its crest. Photo courtesy of Tatiany Oliveira da Silva.



Figure 6. *Afrotrilepis pilosa* (grass) on an inselberg in West Africa. Photo by Stefan Porembski, through Creative Commons.



Figure 7. Sandstone rock outcrop at Fouta Djallon, Guinea. Photo by Maarten van der Bent, through Creative Commons.

Inuthail and Sridith (2010) examined the structure of plant communities on the granitic inselberg in Songkhla Province in Peninsular Thailand. They identified seven microhabitat types: rock crevices and clefts (Figure 8), rock falls (Figure 7), shallow depressions (Figure 2), deep depressions, exposed rock slopes (Figure 4), shady flat rocky slopes (Figure 3, Figure 9), and rock platform fringes. They recorded 73 species of tracheophytes, with Orchidaceae, Rubiaceae, and Poaceae predominating. The highest number of plant species occurred on the fringes of the rock platforms where soil conditions and light intensities vary.



Figure 8. Mosses in fissure of rock outcrop, Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 9. Rock outcrop with shade provided by tracheophytes at Sítio Pedra das Moças, Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Although some researchers disagree about which formations belong to the inselberg category, Porembski *et al.* (1997) considered granitic inselbergs to be present in all the climatic and vegetational zones of the tropics. Because of the harsh edaphic and microclimatic conditions, the vegetation of inselbergs differs greatly from that of their surroundings. The habitats on these rocks can be defined by vegetation groups including cryptogamic crusts, rock pools, monocot mats, and ephemeral flush vegetation. **Stochastic** (randomly determined) environmental disturbances promote greater species richness due to prevention of competitive exclusion. Other processes are deterministic, creating high temperatures and light levels and extended periods of drought. Moss cushions are able to take advantage of seepage water. In West Africa, *Bryum arachnoideum* (Figure 10) is able to take advantage of such wet areas (Frahm & Porembski 1994).



Figure 10. *Bryum arachnoideum*, a moss that colonizes wet seepage areas on rock outcrops in West Africa. Photo by Jan-Peter Frahm, with permission.

Sarthou *et al.* (2009, 2017) described tropical inselbergs as rocky outcrops protruding from a plain landscape. These are hot spots of plant and animal biodiversity that result from the high turnover of species between sites and the presence of organisms mostly

restricted to the inselberg habitat. Thus they are isolated patches of tracheophytic vegetation surrounded by bare rock or cryptogamic vegetation (algae, lichens, and bryophytes).

Sarthou and Villiers (1998) remind us that tropical inselbergs are surrounded by rainforest, but that they have their own special vegetation. They describe six such associations on French Guianan inselbergs. These respond to different environmental characteristics, including local relief, insolation, water availability, and soil depth. Species diversity is low in all of these associations. They found striking similarities in the vegetation units when comparing those of South American and African inselbergs.

It is only recently that ecological studies of bryophytes on inselbergs have emerged. Ribeiro *et al.* (2007) provided a comprehensive summary of vegetation on rock outcrops in Brazil and outlined the three needs they considered most urgent for study:

1. inselbergs and high mountains in the Amazon and the Brazilian northeast
2. long-term studies, which are almost totally unavailable, hindering global change monitoring and assessment
3. national and international networking to speed up scientific production about such habitats.

Frahm (2000) summarized early studies in the volume by Barthlott and Porembski on inselbergs. Valente and Pôrto (2006) described the bryophytes from a rocky outcrop in Bahia, Brazil. Even in 2018, Peñaloza-Bojacá *et al.* (2018a, b) commented on the paucity of bryophyte studies on rock outcrops and inselbergs.

To elucidate outcrop vegetation in the northeastern Brazil, Silva *et al.* (2014a, b) looked at both tracheophytes and bryophytes on rocky outcrops there. They noted that for these small plants, the large outcrops served as islands amid a "sea" of soil, resulting in a floristic composition that results from **stochastic processes** (unpredictable events) at a regional scale. However, such stochastic processes did not show any clear relationship with the communities on a local scale.

Adaptations

Watson (1933) gave an early view of adaptations to terrestrial adaptations of bryophytes. He suggested that these included **cushion** life forms, the arrangement of the leaves to be imbricated or twisted upon drying, hair points or hyaline leaf apices, leaf borders, infolded leaf margins, thickened cell walls, cell size, and papillae. Some store water and others prevent evaporation. Capillarity was accomplished by spaces between leaves, at leaf axils, between leaf folds, and specialized water folds (lobules as in *Frullania*; Figure 11-Figure 12) and storage cells as in *Leucobryum* (Figure 13). Although at that time there was little experimental evidence to support his suggestions, we now find that these traits often describe adaptations of bryophytes of rock outcrops and inselbergs.



Figure 11. *Frullania gibbosa* on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

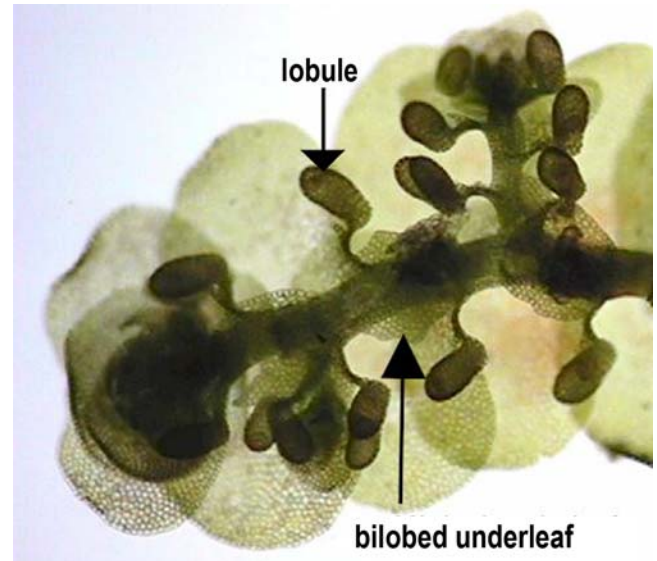


Figure 12. Underside of a *Frullania* branch, showing lobules. Photo by Paul Davison, with permission.



Figure 13. *Leucobryum cf. giganteum* on rock in the Neotropics. Photo by Michael Lüth, with permission.

Life Cycle Strategies

Life cycle strategies can be particularly important in these severe environments. As noted by Benassi *et al.* (2011) for the desert moss *Syntrichia caninervis* (Figure 14), those in the most extreme environments have lower frequencies of sexual expression, fewer sexual branches per individual, and a lower male:female ratio. Sexual reproduction is infrequent. They suggested that male rarity may be due to a lower desiccation tolerance in males. Males have a higher energetic requirement for their sex expression, and this may make them less tolerant to repeated cycles of hydration and desiccation. While rock outcrops and inselbergs are not deserts, many of their microclimate characteristics are similar, so we might expect similar life cycle restrictions.



Figure 14. *Syntrichia caninervis* (Pottiaceae), a xerophytic moss that has lower frequencies of sexual expression, fewer sexual branches per individual, and a lower male:female ratio. Photo by John Game, through Creative Commons.

Frahm (1996) found that bryophytes from the inselbergs he examined in the Ivory Coast and Zimbabwe had a conspicuous lack of both sexual and vegetative propagules. They lacked both the animal and wind dispersal found in inselberg tracheophytes.

Kürschner (2003) found that the life strategy for the *Riccia* liverwort association on thin soil over volcanic rock in Yemen was that of a **shuttle** species. These liverworts produce large spores with short-range dispersal. Disturbances could result in exposure of these spores that have been stored in the diaspore bank. **Geophytes** (plants with short, seasonal lifestyle and some form of underground storage organ) and colonists also occur, but are of only minor importance.

Kürschner (2006) elucidated the ecology of the **saxicolous** (growing on rocks) *Grimmia ovalis* (Figure 15)-*G. laevigata* (Figure 16-Figure 17)-*G. longirostris* (Figure 18) association on Socotra Island of Yemen. The bryophytes on these sun-exposed, acidic rock formations appear to be mostly endemic and are dominated by *Schlotheimia balfourii* (see Figure 19). The life strategy is that of drought-tolerant **cushions**, **short turf**-forming generative **perennial shuttle species**, **perennial stayers**, and **pauciennial** (short-lived) **colonists**.



Figure 15. *Grimmia ovalis* with capsules, a rock dweller on Socotra Island. Photo by Michael Lüth, with permission.

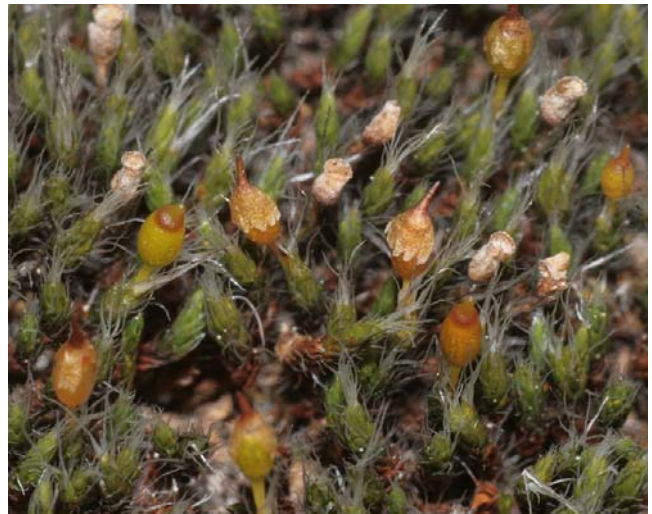


Figure 16. *Grimmia laevigata* with capsules, a rock dweller on Socotra Island. Photo by Hermann Schachner, through Creative Commons.



Figure 17. *Grimmia laevigata*, dry, a rock dweller on Socotra Island. Photo by Janice Glime.



Figure 18. *Grimmia longirostris* with capsules, a rock dweller on Socotra Island. Photo by Hermann Schachner, through Creative Commons.



Figure 19. *Schlotheimia* sp. from the Neotropics; *Schlotheimia balfourii* is a rock dweller on Socotra Island. Photo by Michael Lüth, with permission.

In her study of bryophytes on rock outcrops in Brazil, Silva found that most species were monoicous (26 spp. compared to 20 dioicous species) (Silva 2012; Silva *et al.* 2014b). Nevertheless, the three most frequent species were dioicous. But of these three, two rarely produced sporophytes and one had them only occasionally.

Peñaloza-Bojacá *et al.* (2018a) found that asexual reproduction was important for several of the key species of mosses on Brazilian ironstone outcrops. Surprisingly, dioicous mosses had the highest sexual expression and reproductive success, with most of these species having a female bias. Of the 108 species, 70% were reproducing. A total of 50% of the specimens were reproducing either sexually or asexually. Mosses exhibited mostly asexual reproduction, whereas liverworts mostly exhibited sexual reproduction. Of the asexually reproducing species, 31% had gemmae and 69% had other deciduous propagules. Among the dioicous species, the majority had a female bias.

Pôrto *et al.* (2017) specifically studied the life cycle strategies of the widespread moss *Bryum argenteum* (Figure 20) from a rock outcrop in northeastern Brazil. They noted that despite the severe water constraints of the inselbergs, dioicous mosses are able to colonize rock outcrops and inselbergs. Previous researchers had found

that in northeastern Brazilian rock outcrops, only *Bryum argenteum* frequently had sporophytes (Valente & Pôrto 2006; Silva & Germano 2013; Silva *et al.* 2014a, b). This dioicous species has several asexual strategies – axillary bulbils, rhizoidal gemmae (tubers), and caducous shoot apices (Frey & Kürschner 2011), complemented with numerous small spores when it reproduces sexually (Söderström 1994). Despite its asexual options, 93% of the rock outcrop colonies were expressing sex (Pôrto *et al.* 2017). Although there was a slight female bias, the ratio was only 56:44 female to male. The relationship of number of sporophytes to male:female sex ratio is shown in Figure 21.



Figure 20. *Bryum argenteum* with capsules on rock outcrop in Brazil. Photo of Tatiany Oliveira da Silva.

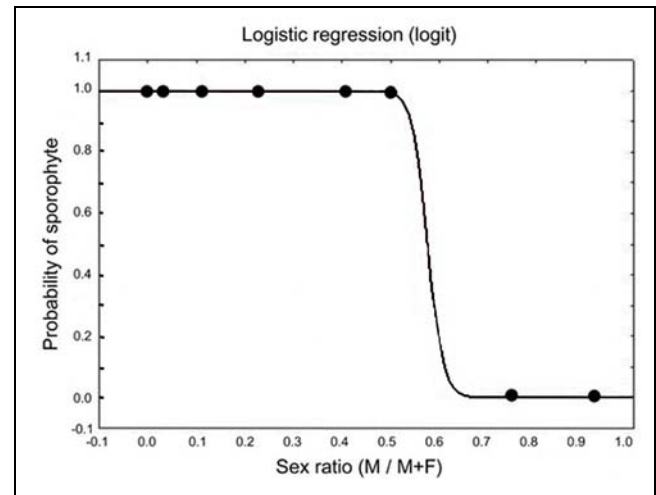


Figure 21. Probability of sporophytes based on sex ratio in *Bryum argenteum*. Modified from Pôrto *et al.* 2017.

So why is *Bryum argenteum* (Figure 20) so productive with sporophytes on the rocks when most other dioicous species are unable to succeed on these rocks? Cronberg *et al.* (2006, 2008) may have the answer. They found that mites are able to disperse the asexual propagules and that springtails (*Collembola*; Figure 22) and possibly mites as well facilitate fertilization. Another factor that may contribute to the success of *B. argenteum* on the rocks and

elsewhere is the ability of antheridia to survive desiccation and rehydration, then to release viable sperm (Shortlidge *et al.* 2012; Stark *et al.* 2016).

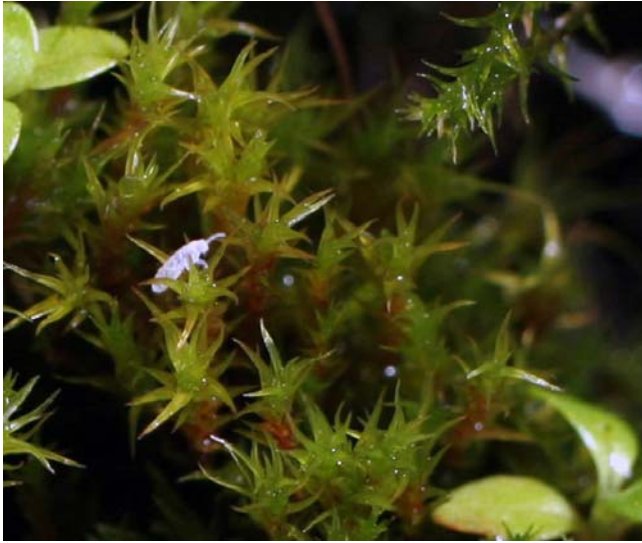


Figure 22. *Folsomia candida* (Collembola) on *Ceratodon purpureus* in fertilization study. Photo courtesy of Erin Shortlidge.

Dispersal

Dispersal can limit the species that reach inselbergs because the surrounding vegetation is of a completely different type (Burke 2002a). Frahm and Porembski (1994) considered the inselbergs of western Africa to be refugia for dry-adapted bryophyte species. Burke (2002a) investigated the role of inselbergs in Namibia as refugia for tracheophyte species. These inselbergs are considered to have a high recolonization potential and a high diversity relative to the landscape. Burke found that gene flow and nutrient flow occur from the inselbergs to the surrounding lowlands. The granite inselbergs support longer-lived species of stable communities, whereas the dolerite inselbergs support transient communities of short-lived species. Regional differences relate to climate, with differences in climate and geology contributing. Altitude is likewise an important variable. Species of granite inselbergs are more closely allied to the surrounding habitats than are those of dolerite inselbergs. Burke concluded that conserving groups of inselbergs is more important to conserving their unique species than conserving isolated mountains. "Stepping stone" inselbergs have greater potential for conserving those species with short dispersal ranges.

These principles should likewise apply to bryophytes, but most likely at a greater distance scale. One way that bryophyte dispersal is facilitated to boulders and inselbergs is having a large number of propagule sources nearby. This can be other boulders and inselbergs, but for many species, it is the ability to grow on other types of substrates. Pócs (1982) demonstrated that many of the tropical species of **Meteoriaceae** (Figure 69-Figure 70), **Neckeraceae** (Figure 23-Figure 24), **Pterobryaceae** (Figure 25), **Plagiochila** (Figure 26), and **Lejeuneaceae** (Figure 37) that are typically corticolous (growing on bark) may also be abundant on rocks.



Figure 23. *Neckera* on rock. Photo by Michael Lüth, with permission.



Figure 24. *Neckera urnigera* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 25. *Calyptothecium duplicatum* (Pterobryaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 26. *Plagiochila* sp. from the Neotropics. Photo by Michael Lüth, with permission.

Desiccation Recovery

One area of adaptations that was usually ignored in early studies was physiological adaptations. Lüttge *et al.* (2008) reported strong quenching of chlorophyll fluorescence in the three desiccated bryophytes in their study of three poikilohydric, homiochlorophyllous moss species from sun-exposed rocks of a Brazilian tropical inselberg. Using *Campylopus savannarum* (Figure 27-Figure 28), *Rhacocarpus fontinaloides* (see Figure 29), and *Ptychomitrium vaginatum* (see Figure 30), they concluded that these species have photo-oxidative protection that permits them to live on exposed rocks that experience high light intensity. They achieve this by a reduction of the base chlorophyll fluorescence to nearly zero. Upon rewetting there is a rapid recovery to higher values in the first 5 minutes, requiring more than 80 minutes to reach equilibrium. These adaptations help to define their niches, with *C. savannarum* forming an inner belt and *R. fontinaloides* forming an outer belt around the vegetation. *Ptychomitrium vaginatum*, on the other hand, lives in small cushions on bare rock. Nevertheless, these three species differ little in their reduction of fluorescence or rewetting recovery and have only slight differences in photosynthetic capacity. The researchers suggest that CO₂ acquisition is a greater problem in *P. vaginatum* than in the other two species, with water films causing limitations in CO₂ uptake.



Figure 27. *Campylopus savannarum* and *C. pilifer* in fissure of rock outcrop in Brazil. Photo by courtesy of Tatiany Oliveira da Silva.



Figure 28. *Campylopus savannarum*, a species that has photo-oxidative protection that helps to adapt it to living in exposed rock habitats. Missouri Botanical Garden, through Creative Commons.

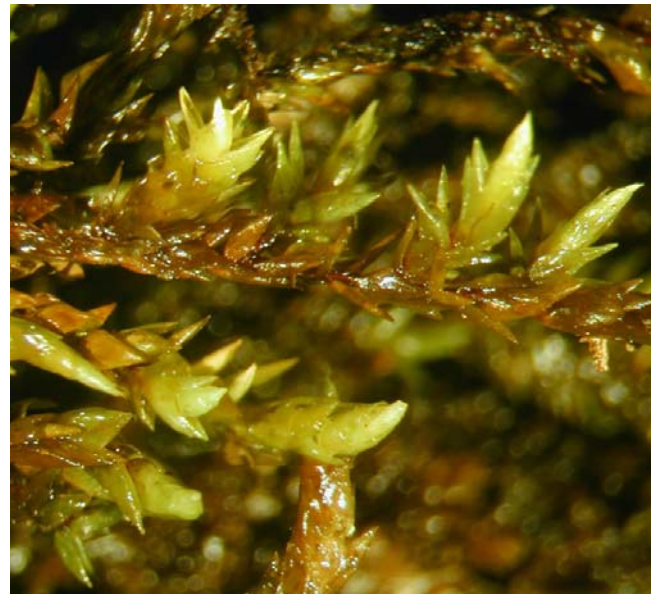


Figure 29. *Rhacocarpus inermis* from the Neotropics; *Rhacocarpus fontinaloides* has photo-oxidative protection that permits it to live on exposed rock surfaces. Photo by Michael Lüth, with permission.



Figure 30. *Ptychomitrium* sp. with capsules; *Ptychomitrium vaginatum* has photo-oxidative properties that help to permit it to live on exposed rocks. Photo by Paul Wilson, with permission.



Figure 31. *Cyanotis lanata*, a species that seems to improve the rock outcrop environment for the moss *Archidium acanthophyllum*. Photo by Anya Quinn, through Creative Commons.



Figure 32. *Archidium ohioense*; in southwestern Nigeria, *Archidium acanthophyllum* occurs on rock outcrops. Photo by Li Zhang, with permission.

Interactions with Other Plants

As noted by During and van Tooren (1990) as a general principle, bryophyte habitats can be defined by not only the physical environment, but also the tracheophyte vegetation associated with it. Nevertheless, at that time few studies had analyzed the functionality of these interactions.

Tracheophytes on boulders and inselbergs collect soil, provide shade, and retain moisture for longer times than unvegetated areas. Protection by the monocot *Cyanotis lanata* (Figure 31) permits *Archidium* (see Figure 32) to survive on savannah rock outcrops in southwestern Nigeria (Egunyomi 1984; Oluwole & Adetunji 2010). [The naming of this *Archidium* has been problematic, with Egunyomi naming it *Archidium ohioense*, then Frahm and Porembski (1994) determining it to be *Archidium globiferum* in West Africa. However, currently it seems to be considered to be *Archidium acanthophyllum*.] During the rainy season, the annual mosses *Bryum argenteum* (Figure 20) and *Pelekium gratum* (Figure 33) may also appear in this association (Egunyomi 1984).



Figure 33. *Pelekium cf. gratum*, a species that often accompanies *Archidium acanthophyllum* on rock outcrops in southwest Nigeria. Photo by Shyamma L., through Creative Commons.

On these southwestern Nigerian inselbergs, there is a three-member association that illustrates relationships among the moss *Archidium acanthophyllum* (see Figure 32), tracheophyte *Cyanotis lanata* (Figure 31), and lichen *Diploicia canescens* (Figure 34) (Oyesiku & Amusa 2010). Oyesiku and Egunyomi (2004) found a frequency of 50% of occurrences of *Archidium acanthophyllum* with *Cyanotis lanata*, whereas only 20% grew alone and 30% grew with other plants, suggesting some benefit from its association with *C. lanata*. But these two species grow best in somewhat different optima. For *C. lanata*, the optimum pH is 6.7, whereas it is 7.7 for *A. acanthophyllum*. *Cyanotis lanata* density increases and *Archidium acanthophyllum* decreases from March to September, whereas both the *A. acanthophyllum* and *C. lanata* decrease from September to December (Figure 35). This is likely due to the strong increase in temperature of the substrate to 39.6°C in December. Both plants are harmed at temperatures above 50°C. In June and September, the relative humidity above the vegetation increases significantly, with a mean of 79% during the study. Data indicate that *C. lanata* and *A. acanthophyllum* facilitate each other. As noted in other ecosystems (e.g. Richardson 1958; Edward & Miller 1977), thick bryophyte growths can serve as insulation to buffer the temperature of the underlying substrate. Richardson (1958) also noted that bryophytes could reduce evaporation. Both of these properties provide a more favorable environment for the roots of tracheophytes. Oyesiku and Egunyomi (2004) verified that these relationships are true for bryophytes on inselbergs.



Figure 34. *Diploicia canescens*, a lichen that occurs on rock outcrops in southwestern Nigeria. Photo by Jymm, through public domain.

On these inselbergs in southwestern Nigeria, the lichen *Diploicia canescens* (Figure 34) maintains a consistent density throughout the year (Oyesiku & Amusa 2010). On the other hand, the monocot *Cyanotis lanata* (Figure 31) and the moss *Archidium acanthophyllum* (see Figure 32) coexist, but in this relationship, the density of *A. acanthophyllum* decreases as that of *Cyanotis lanata* increases from March to September (Figure 35). From September to December, both species decrease (Figure 35). Whereas the moss and monocot seem to facilitate each

other, the lichen is inhibited by growth of these two species.

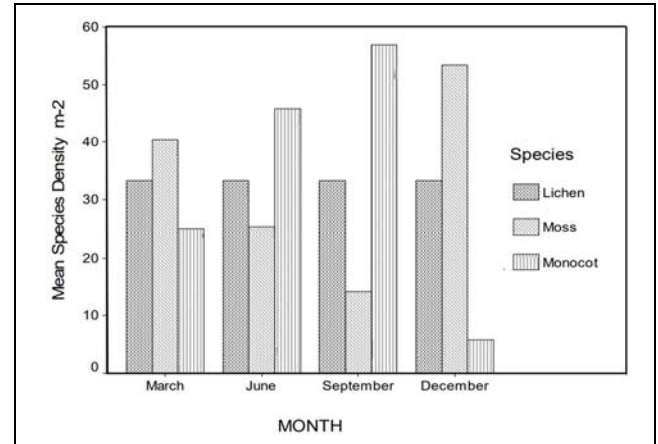


Figure 35. Quarterly density dominance of three interacting plants and lichens on the Baasi Inselberg, Nigeria. Modified from Oyesiku and Egunyomi 2004.

The bryophytes and tracheophytes can also have nutrient cooperation. Bryophytes collect dust and runoff that contain nutrients. These can later be transferred to the tracheophytes. Oyesiku (2018 in press) investigated these relationships between *Archidium acanthophyllum* (see Figure 32) and *Cyanotis lanata* (Figure 31).

Lava Flows

Tropical lava flows provide unique rock habitats. Ah-Peng *et al.* (2007) investigated the altitudinal differences on a recent lava flow (19 years old) on Réunion Island. Because of the uniformity of the lava flow, it is easier than in most habitats to isolate variables such as altitudinal effects. They surveyed bryophyte communities from 250 to 850 m asl using the three substrates of ground and rachises of two fern species. As in many other altitudinal studies, bryophyte diversity increased with altitude. They identified 70 species of bryophytes in the study, with diversity related to microhabitats. The lava flows support a high number of pioneer organisms that are able to colonize remnant lowland rainforest.

Richness and Diversity

Rocky outcrops and inselbergs form islands amid the surrounding soil vegetation (Silva *et al.* 2014a, b), although Silva and coworkers did not compare the flora of the inselbergs with the surrounding vegetation. If they are correct, the species that arrive there must often come from a distance and must rely on **stochasticity** (unpredictable events). Silva and coworkers demonstrated that such processes are the major factors determining species clustering at a regional scale. Such a relationship was not clear at the local level.

Later, Sarthou *et al.* (2017) provided us with evidence that the surrounding forest, regional climate, and inselberg features including altitude, shape, habitats, summit vegetation, epiphytism, and fire events contribute to shifts in the distribution of species and functional traits. These factors determine the floristic patterns on inselbergs in French Guiana and demonstrate that the surrounding forest

can contribute to the inselberg vegetation. This is probably even more likely for bryophytes.

Ribeiro *et al.* (2007) often found xerophytes and hydrophytes (of the tracheophytes) side-by-side on the boulders due to the small scale environmental heterogeneity. Such conditions also support the great variety of bryophytes on these rocks.

Africa

The inselbergs of West Africa are geologically old and typically dome-shaped monoliths (Porembski & Barthlott 1996). The vegetation differs starkly from that of the surrounding vegetation. The inselbergs provide a severe climate with extreme temperatures and light intensity. Nevertheless, ~600 tracheophyte species occur among these inselbergs, predominately in the grasses (Poaceae), sedges (Cyperaceae), and legumes (Fabaceae). The rocks provide such habitats as cryptogamic crusts, rock pools, monocotyledonous mats, and ephemeral flush vegetation that can be distinguished based on physiognomy (Porembski *et al.* 1997). The ephemeral flush vegetation is the richest in species (Porembski & Barthlott 1996). Moss cushions, particularly those of *Bryum arachnoideum* (Figure 10), can establish where seepage water is sufficient (Frahm & Porembski 1994).

The tracheophytes on Ivory Coast inselbergs exhibit low **beta diversity** – that is, the flora is relatively uniform across the country (Porembski & Barthlott 1996). Higher beta diversity occurs in the small habitats like rock pools, presumably due to stochasticity. Diversity decreases from savannahs toward the rainforest zone. In the drier areas in the northern part of the Ivory Coast, the growing conditions are less favorable, permitting weak competitors to have a better chance.

On the tropical inselbergs of the Ivory Coast (Côte d'Ivoire) (Figure 36) and Zimbabwe, Frahm and coworkers found that the number of bryophyte species does not correlate with either size of inselberg or elevation (Frahm 1996; Frahm *et al.* 1996). In the Ivory Coast, species richness is greater when the inselberg is in the savannah compared to those in rainforest regions. In the Ivory Coast, they found total species richness of inselbergs to be 31, whereas in Zimbabwe it was only 25. Only 3 families are represented. These researchers found that inselberg bryophytes have larger distribution areas and no endemic species compared to tracheophytes on them. Eight species are common to both. One interesting feature is that these bryophytes typically lack sexual reproduction, but have "conspicuous" vegetative reproduction.

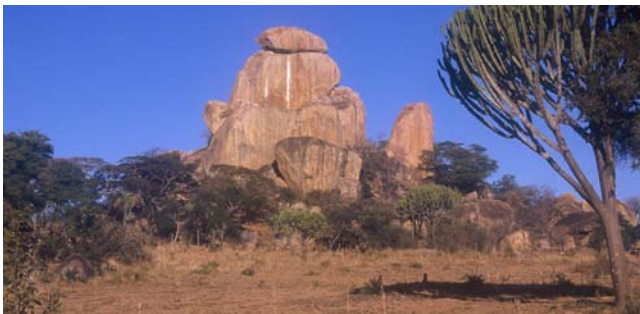


Figure 36. Inselberg (kopje) in Marada Hills, Zimbabwe. Photo by Kevin Walsh, through Creative Commons.

The highest number of bryophyte species from African inselbergs was in the Côte d'Ivoire with 31 species, contrasting with the lowest number of 16 in the Seychelles. This can probably be explained by the location of Côte d'Ivoire in the rainforest as well as in the savanna belt, widening the surrounding vegetation types. Most of the species of bryophytes are acrocarpous mosses, with only *Sematophyllum fulvifolium* and *Erythrodontium squarrosus* representing the pleurocarpous mosses.

Frahm and Porembski (1997) visited the small tropical African country of Benin. They identified 8 liverworts and 10 mosses from inselbergs. Of these, 5 liverworts [*Acrolejeunea emergens* (Figure 37), *Riccia atropurpurea* (Figure 38), *R. congoana* (Figure 39), *R. discolor*, *R. moenkemeyeri*] and all of the mosses [*Archidium ohioense* (possibly *A. acanthophyllum*; Figure 32), *Brachymenium acuminatum* (Figure 40), *B. exile* (Figure 41), *Bryum arachnoideum* (Figure 10), *B. argenteum* (Figure 20), *Bryum depressum*, *Garckea moenkemeyeri* (see Figure 42), *Hyophila involuta* (Figure 43-Figure 44), *Philonotis mniobryoides* (see Figure 58) and *Weissia cf. edentula* (Figure 45)] proved to be new records for the country. This may relate more to lack of studies than to uniqueness of the inselbergs.

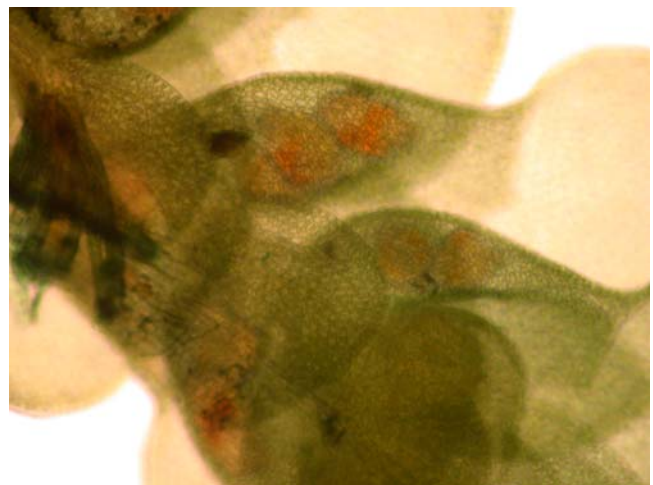


Figure 37. *Acrolejeunea emergens* (Lejeuneaceae) with rotifers (reddish). Photo courtesy of Claudine Ah-Peng.



Figure 38. *Riccia atropurpurea*, a liverwort that occurs on inselbergs in Benin, Africa. Photo from Missouri Botanical Garden, through Creative Commons.



Figure 39. *Riccia congoana*, a liverwort that occurs on inselbergs in Benin, Africa. Photo from Missouri Botanical Garden, through Creative Commons.



Figure 40. *Brachymenium acuminatum*, a moss that occurs on inselbergs in Benin, Africa. Photo by Jan-Peter Frahm, with permission.



Figure 41. *Brachymenium exile*, a moss that occurs on inselbergs in Benin, Africa. Photo by Show Ryu, through Creative Commons.



Figure 42. *Garckea flexuosa*; *Garckea moenkemeyeri* is a moss that occurs on inselbergs in Benin, Africa. Photo by Manju C. Nair, through Creative Commons.



Figure 43. *Hyophila involuta* habitat in India. Photo by Michael Lüth, with permission.



Figure 44. *Hyophila involuta*, a moss that occurs on inselbergs in Benin, Africa. Photo by Michael Lüth, with permission.



Figure 45. *Weissia edentula* with capsules, a moss that occurs on inselbergs in Benin, Africa. Photo by Louis Thouvenot, with permission.

Burke (2002b) found that in Namibia, soil properties do not seem to have an important role in the arid environments. Furthermore, parameters such as slope aspect and angle play a minor role. The grassland and shrubland plant communities relate primarily to general habitat, elevation, size of inselberg, and geology. The inselbergs are able to harbor plant species from neighboring higher rainfall areas, thus providing a propagule source for recolonization.

Burke (2003) found that granite inselbergs in Namibia are more closely related to mountain habitats than are the dolerite ridges. And as expected, higher inselbergs are more closely related to mountain habitats than are lower inselbergs. Many species, especially those with broad habitat requirements, are common to both inselbergs and mountain habitats. On the other hand, the short-lived transient species are more similar between the dolerite ridges and the "mainland." Thus, the granite inselbergs can be important sources of remnant populations from a wetter past, whereas the dolerite ridges can form species pools for the rangeland.

Kürschner (2003) extended our knowledge of rock outcrops in the Jabal Arays area of Yemen. Here they found communities of *Riccia jövet-astiae* (see Figure 38-Figure 39) and *Riccia argenteolimbatae* on the thin soils overlying volcanic rock outcrops in monsoon areas where woodlands are characterized by *Sterculia africana* (Figure 46). These are typically accompanied by *Mannia androgyna* (Figure 47) and *Barbula unguiculata* (Figure 48-Figure 49). The shallow soils generally have large numbers of riccioid and marchantioid liverworts, with *Riccia atromarginata*, *R. albolimbata* (Figure 50-Figure 51), and *R. argenteolimbata* characterizing the association.

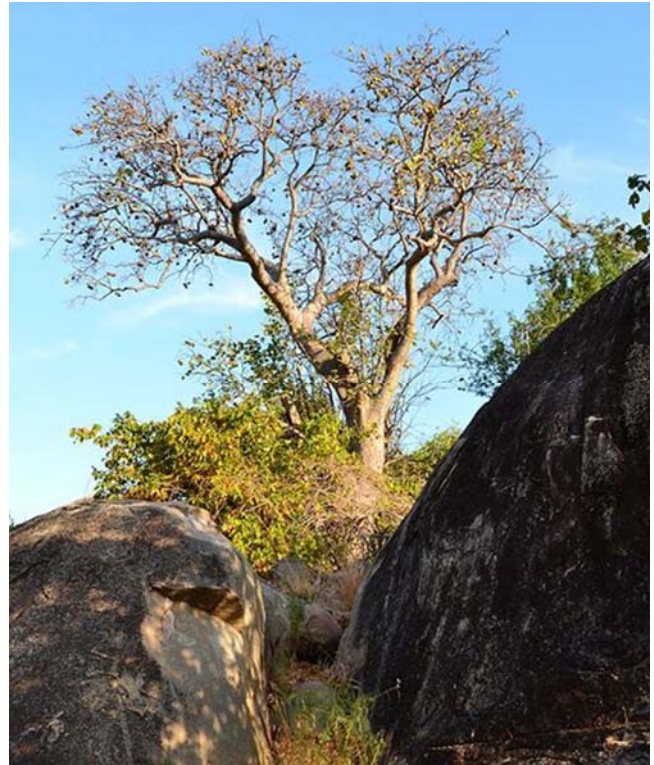


Figure 46. *Sterculia africana* in Malawi. Photo by Jinge Norvall Andrews, through Creative Commons.



Figure 47. *Mannia androgyna*, a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Valter Jacinto, through Creative Commons.



Figure 48. *Barbula unguiculata* (dry), a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Bob Klips, with permission.



Figure 49. *Barbula unguiculata* with capsules (wet), a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Michael Lüth, with permission.



Figure 50. *Riccia albolimbata* (dry), a species of rock outcrops in the Jabal Arays area of Yemen. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

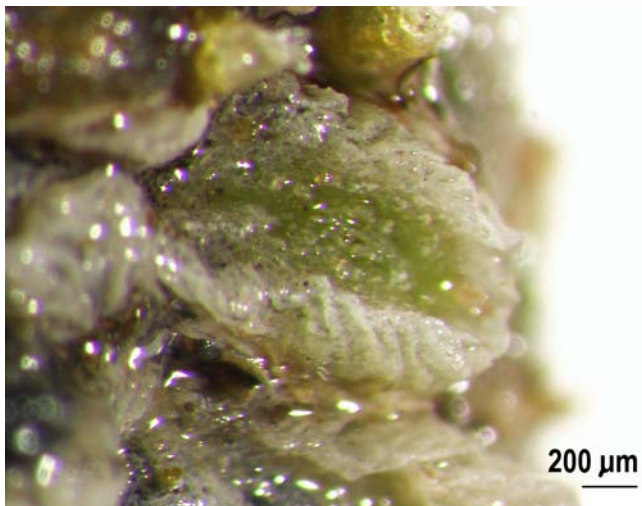


Figure 51. *Riccia albolimbata* (wet), a species of rock outcrops in the Jabal Arays area of Yemen. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In the Drakensberg area of South Africa, Hodgetts *et al.* (1999) found that lowland sandstones support common and widespread species that can survive long drought periods. More species are present where there is more moisture, as in ravines, rock crevices, and on stream banks. A different suite of species occur on shaded sandstone cliffs and rocks. A third type of community occurs in flushes. Exposed rocks generally have few species, with *Grimmia pulvinata* (Figure 52) and *Ptychomitrium cucullatifolium* (Figure 53) being common here. On the basalt rocks, at about 3,000 m asl, most species are restricted to crevices, on boulders, and in the turf below the cliffs. *Quathlamba debilicostata* (in narrow cracks) and *Orthotrichum oreophilum* (in cushions on inner vertical and overhanging surfaces of wider cracks; Figure 54) seem to occur only in vertical cracks in the basalt cliffs.



Figure 52. *Grimmia pulvinata* with capsules, a species of exposed rocks in tropical South Africa. Photo by Michael Becker, through Creative Commons.



Figure 53. *Ptychomitrium polyphyllum* with capsules; *Ptychomitrium cucullatifolium* is a species of exposed rocks in tropical South Africa. Photo by David T. Holyoak, with permission.



Figure 54. *Orthotrichum* sp. on vertical rock; *Orthotrichum oreophilum* occurs on the inner vertical surfaces of wide cracks of inselbergs. Photo by Algirdas, through public domain.

Neotropics

Porembski *et al.* (1998; Porembski 2007) defined **inselbergs** as "mostly" dome-shaped rock outcrops in all climatic and vegetational zones of the tropics. In Brazil, these consist of Precambrian granites and gneiss that form ancient and stable landscape elements. Because of their exposure, they create harsh conditions of microclimate. These strikingly different conditions result in strikingly different vegetation. One of the most characteristic communities is one of monocotyledonous mats. These can provide cover and retain moisture that permits some bryophytes to survive there. Porembski and coworkers, studying tracheophytes, found that the alpha diversity (community diversity) of the mats differed little among the six outcrops studied. However, beta diversity (regional) differed greatly between sites. The Brazilian rock outcrops demonstrate a higher diversity compared to those of West African inselbergs, with the appearance of more endemics in the Brazilian communities. However, some species considered endemics at that time may have proved to be synonyms of more widespread species since then. Nevertheless, the diversity is high, perhaps due to the large species pool.

Silva (2012) studied the rock communities in the state of Pernambuco, Brazil. She divided the microhabitats on the outcrops into exposed rock, fissure, soil island, and **cacimba** (rock pools – pit in wet or marshy ground, collecting the water present in the soil that accumulates in it by condensation). Substrates also differed: rock, live

trunk, dead trunk, and soil. She identified 49 species in 36 genera and 20 families. Of these, 34 were mosses, 15 were liverworts. The most species-rich families were the leafy liverworts **Lejeuneaceae** (Figure 37) (7 spp) and **Frullaniaceae** (Figure 55) (4 spp), and the moss families **Bryaceae** (Figure 20) (6 spp), **Dicranaceae** (Figure 27-Figure 28, Figure 56) (4 spp), and **Pottiaceae** (Figure 14) (4 spp), comprising 53% of the species. The liverwort genus *Frullania* (Figure 55) and moss genus *Campylopus* (Figure 56) had the highest species richness. The most common species were the mosses *Brachymerium exile* (Figure 57), *Bryum argenteum* (Figure 20), *Campylopus pilifer* (Figure 56), *C. savannarum* (Figure 27-Figure 28), *Philonotis hastata* (Figure 58), and *Syrrhopodon gaudichaudii* (Figure 59-Figure 60), and the liverworts *Frullania kunzei* (Figure 55) and *Riccia vitalii* (Figure 61); frequencies are in Table 1. Two of the less common species, *Atractylocarpus brasiliensis* (see Figure 62) and *Riccia taeniiformis* (Figure 63), are endemic to Brazil. **Turf** comprised 74% of the life forms. The most species richness (37 spp., 89%) occurred on soil islands that were 1.0 and 4.9 cm deep, whereas only 12 species occurred on rock. Approximately half the species had a wide distribution pattern. Similarity among sites was less than 50%.

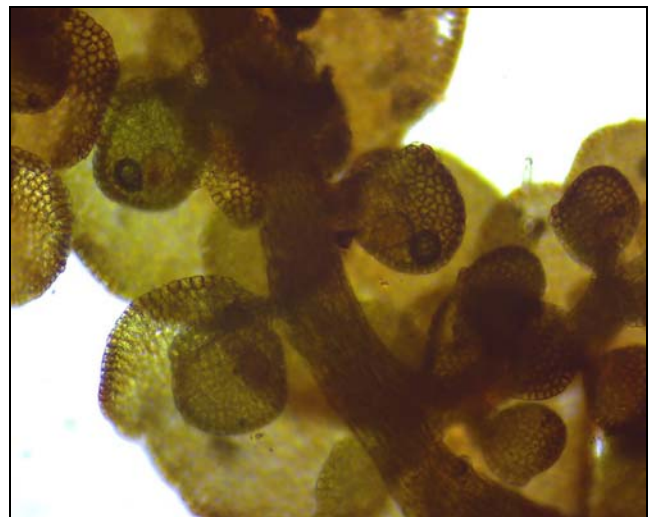


Figure 55. *Frullania kunzei*, a frequent rock outcrop species in Brazil. Photo by Y. Inturias, through Creative Commons.



Figure 56. *Campylopus pilifer* on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 57. *Brachymenium exile*, one of the most common species on rock outcrops in Brazil. Photo by Show Ryu, through Creative Commons.



Figure 60. *Syrrhopodon gaudichaudii* demonstrating the leaf curling that helps it conserve water on exposed rocks. Photo by Juan David Parra, Creative Commons.

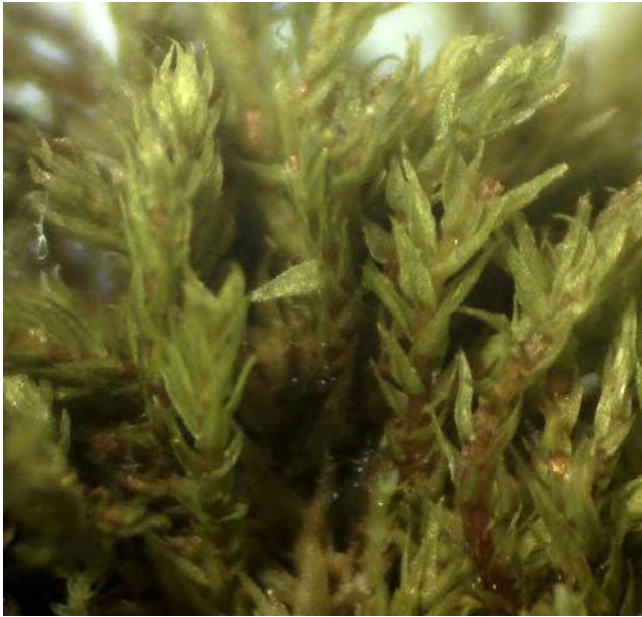


Figure 58. *Philonotis hastata*, a common species on rock outcrops in Brazil. Photo by Y. Inturias, through Creative Commons.



Figure 61. *Riccia vitalii*, a common liverwort on rock outcrops in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 59. *Syrrhopodon gaudichaudii*, on a rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 62. *Atractylolcarpus madagascariensis*; *Atractylolcarpus brasiliensis* occurs on rock outcrops in Brazil, where it is endemic. Photo by Jan-Peter Frahm, with permission.



Figure 63. *Riccia taeniiformis* on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 65. *Barbula indica*, a common species on rock outcrops in Brazil. Photo by Jan-Peter Frahm, with permission.

Table 1. The most common bryophyte species on rock outcrops in Brazil (Silva 2012).

Species	Frequency
<i>Campylopus savannarum</i> (Figure 27-Figure 28)	97
<i>Campylopus pilifer</i> (Figure 56)	52
<i>Bryum argenteum</i> (Figure 20)	30
<i>Frullania kunzei</i> (Figure 55)	15
<i>Philonotis hastata</i> (Figure 58)	14
<i>Syrrhopodon gaudichaudii</i> (Figure 59-Figure 60)	14
<i>Barbula indica</i> (Figure 64-Figure 65)	13
<i>Brachymenium exile</i> (Figure 57)	13
<i>Riccia vitalii</i> (Figure 61)	12
<i>Octoblepharum albidum</i> (Figure 66)	10



Figure 66. *Octoblepharum albidum*, a common species on rock outcrops in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 64. *Barbula indica* on rock in Bareilly India. Photo by Michael Lüth, with permission.

Like Silva (2012), when studying Brazilian ironstone outcrops Peñaloza-Bojacá *et al.* (2018a) found the greatest bryophyte diversity on soil, but also on the rocks. They identified 108 species of bryophytes (42 liverworts and 66 mosses). In Cangas sites, Peñaloza-Bojacá *et al.* (2018b) reported 96 bryophyte species from Brazilian ironstone outcrops. These were comprised of 56 mosses and 40 liverworts, with 68 of the species associated with tree microhabitats and 67 species with bark substrates. The ironstone sites seem to harbor more species than other types of rock outcrops in the country.

Silva and Germano (2013) studied rock outcrops in the caatinga biome in the state of Paraíba, Brazil, from February 2010 to May 2011 and identified 21 bryophyte species, 6 liverworts and 15 mosses. They were able to identify three species clusters. These were **generalist** species that required high light. Their leaf structures generally permitted them to withstand drying environmental conditions.

In their study of the campos rupestres of Chapada Diamantina, Bahia, Brazil, Bastos *et al.* (2000) identified 65 taxa (41 moss species, 24 liverwort species) comprising a total of 20 families. Most of these taxa seem to be restricted to the Chapada Diamantina and are not known from other parts of the state.

Sarthou *et al.* (2009) examined the factors that have a role in the seral stages on the inselbergs in French Guiana. The environment is harsh, with violent storms, intense runoff, and lightning strikes, destroying vegetation cover and organic matter. They considered the vegetational changes to be truly successional, not conditioned by slope. The vegetation experienced cyclic changes that were reinitiated by fire (lightning), wood-destroying fungi, and termites that destroyed the vegetation.

In her inselberg succession studies, Sarthou and coworkers (2009, 2017) found that where the aerial parts of *Clusia minor* (Figure 67) have been destroyed, the ground frequently is covered with mosses and lichens. Their rhizoids capture and retain soil particles, preventing them from being flushed away by water.



Figure 67. *Clusia minor*, an inselberg species that is replaced by mosses and lichens when it is destroyed by fire or other disturbance. Photo by David J. Stang, through Creative Commons.

Sarthou *et al.* (2017) compared 22 inselbergs in French Guiana. They found that the spatially dictated environmental gradient was a primary driver in the floristic composition on these inselbergs. Southward communities have more drought-adapted plants. The northern group has high endemism. The north-south gradient is driven by regional climate (annual rainfall), forest matrix (canopy openness), and inselberg features (altitude, shape, habitats, summit forest, degree of epiphytism, fire events).

Breen (1953) studied bryophytes in subtropical Florida, USA. She found that a number of tropical species occurred exclusively on limestone in subtropical Florida (and in many cases other southern states). Tropical *Jaegerinopsis* (Pterobryaceae), *Vesicularia* (Hypnaceae; Figure 68), *Meteoriopsis* (Figure 69), *Papillaria* (Figure 70), and *Syrrophodon* (Figure 59-Figure 60) are restricted mostly to hammocks, usually on bark of 1-2 species of hardwoods. In swamps, *Cyclodictyon* (Figure 71) and some tropical *Fissidens* (Figure 72) occur. But the limestone regions hold the most bryologically interesting species. Most of the coastal land in the Caribbean and in the West Indies is of limestone origin. She found 11 Neotropical species that in Florida are restricted to limestone. *Luisierella barbula* is a tiny species easily overlooked, but is relatively widespread in Central America and Brazil. *Hyophiladelphus agraria* (see Figure 73) is widespread in both the Neotropics and subtropics. *Weissia*

jamaicensis (Figure 74) occurs in some Central American countries as well as Florida; it is sterile in Florida. This species typically occurs there with *Marchantia paleacea* (Figure 75). *Hypopterygium tamarisci* (Figure 76) is a tropical relic in Florida, also known from both Central and South American tropics. *Leptodictyum riparium* (Figure 77), also a Floridian limestone dweller, is more widespread in aquatic habitats, but is known from Mexican tropics. *Gymnostomiella vernicosa* (Figure 78-Figure 79) is also in Jamaica, Haiti, and Mexico. *Plaubelia sprengelii* (Figure 80) also occurs in the West Indies, Mexico, and Central America, whereas *Syrrophodon prolifer* (Figure 81) occurs in these locations plus South America, typically on thin layers of soil over limestone in protected pockets. *Taxiphyllum cuspidatum* (see Figure 82) occurs on boulders. *Hyophila involuta* (Figure 43-Figure 44) is a common tropical rock dweller, but is again restricted to limestone in Florida. *Fissidens hallianus* (see Figure 72) is restricted in the USA to Florida. The other species Breen found on the Floridian limestone are not tropical.



Figure 68. *Vesicularia vesicularis* var. *vesicularis* from the Neotropics. *Vesicularia* occurs on limestone rocks in Florida, USA. Photo by Michael Lüth, with permission.



Figure 69. *Meteoriopsis squarrosa*; the genus *Meteoriopsis* is restricted mostly to bark in hammocks in Florida. Photo by Manju Nair, through Creative Commons.



Figure 70. *Papillaria crocea*; *Papillaria* is restricted mostly to bark in hammocks in Florida. Photo by Peter Woodard, through public domain.



Figure 71. *Cyclodictyon albicans* with capsules, in a tropical genus that also occurs in Florida, USA. Photo by Claudio Delgadillo Moya, with permission.



Figure 72. *Fissidens asplenioides* from the Neotropics, in a genus found in swamps in Florida. Photo by Michael Lüth, with permission.



Figure 73. *Hyophiladelphus* sp. with capsules; *H. agraria* is a Neotropical species that in Florida is restricted to limestone. Photo by Fred Essig, with permission.

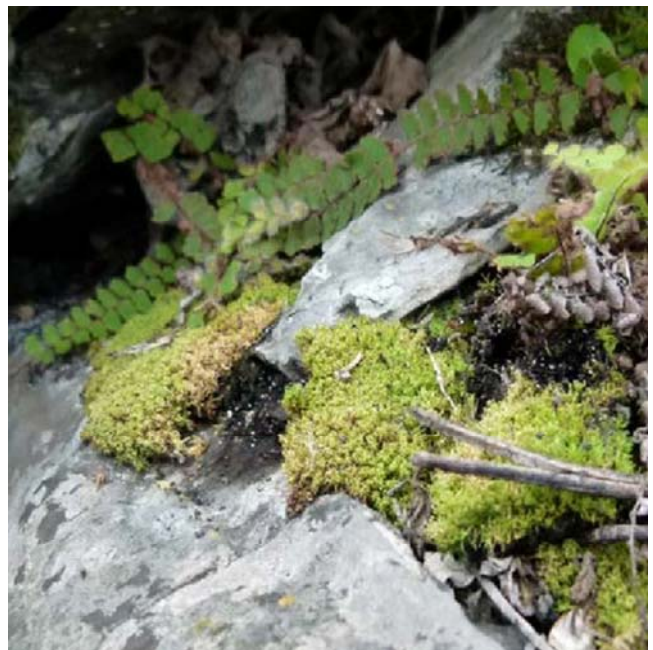


Figure 74. *Weissia jamaicensis* on limestone rock bands, Uige Province, Angola, a species that also occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by T. Lautenschläger, through Creative Commons.



Figure 75. *Marchantia paleacea*, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by David Long, with permission.



Figure 78. *Gymnostomiella vernicosa tenerum*, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Sean Edwards, with permission.



Figure 76. *Hypopterygium tamarisci*, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by Peter Woodard, through Creative Commons.



Figure 79. *Gymnostomiella vernicosa tenerum* gemma, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Sean Edwards, with permission.



Figure 77. *Leptodictyum riparium*, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by Michael Lüth, with permission.



Figure 80. *Plaubelia sprengelii*, a species that occurs on limestone rocks in Florida, USA, and the in Neotropics. Photo by Jan-Peter Frahm, with permission.

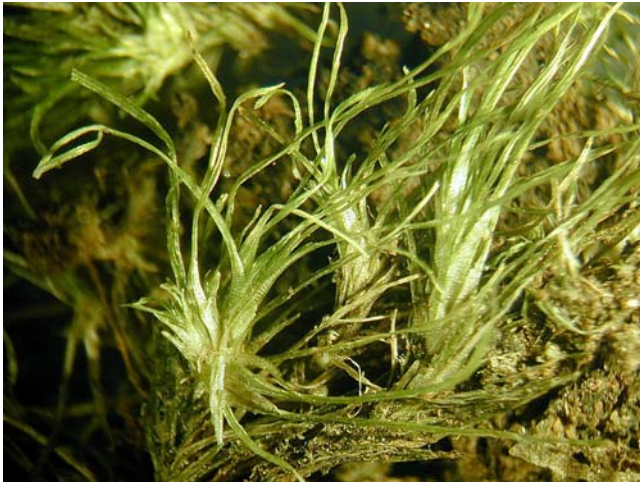


Figure 81. *Syrrhopodon prolifer* var. *scaber* from the Neotropics, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Michael Lüth, with permission.



Figure 82. *Taxiphyllum taxirameum* with capsule; *Taxiphyllum cuspidatum* occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Bob Klips, with permission.

Conceição and Pirani (2005) noted the lack of quantitative studies in tropical cave habitats. They compared outcropping, intertidal, and trench habitats, and found that when different types of habitats are contiguous, there is greater heterogeneity of both strata and life forms in a restricted area, supporting more species. Their study was not based on bryophytes, but it would be interesting to test this hypothesis on the bryophytes.

Summary

Inselbergs (abrupt rock outcrops) and other rock formations are typically xeric and have unique vegetation surrounded by vegetation of a different type, often isolating them like an island. Temperatures and water availability can vary widely, and exposure to high light intensity is common. The bryophytes, and even the tracheophytes, are typically **poikilochlorophyllous mats**). Differing niches are created by fissures and crevices, pockets where water collects, tracheophyte shade, and vertical faces that are shaded or exposed.

Limited competition permits **stochastic** processes to determine communities. Surprisingly, inselberg vegetation units of South America and Africa are similar.

Moss **cushions** are common. Adaptations such as hyaline tips and awns protect against UV light during dry periods. Leaves often twist when dry, have infolded leaf margins, thickened cell walls, small cells, and papillae to protect against UV damage and to retain water longer. Lobules help to store water in some leafy liverworts. Mosses such as *Leucobryum* have hyaline cells that store water and protect the chlorophyll. Sexual reproduction is infrequent. Photo-oxidative protection protects chlorophyll from UV light when dry. *Riccia* species on thin soil produce large spores with short-range dispersal and storage in diaspore banks, permitting them to be **shuttle** species. Other bryophytes are drought-tolerant **cushions**, **short turf-forming perennial shuttle species**, **perennial stayers**, and **pauciennial colonists**. Mosses are more likely to have asexual reproduction, whereas liverworts mostly exhibit sexual reproduction. *Bryum argenteum* is a common rock resident that frequently has sporophytes, perhaps due to sperm dispersal by springtails and mites. It is important to conserve groups of inselbergs to facilitate stepping stone dispersal. For others (e.g. **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, *Plagiochila*, and *Lejeuneaceae*), having other suitable substrates increases dispersal potential.

In some cases the bryophytes retain moisture and collected nutrients that provide for the tracheophyte roots, whereas the tracheophyte provides shade that cools the bryophytes and protects from UV damage, as seen in the moss *Archidium globiferum* and the shrub *Cyanotis lanata*.

In Africa, inselbergs surrounded by savannah have a higher species richness than when forests surround them. Inselbergs can harbor recolonization sources for surrounding disturbed dry habitats. Asexual reproduction predominates. Leafy liverworts seem to be more common on the Neotropical rock outcrops than on the African inselbergs. *Riccia* species are common on thin soils in both areas. Having trees and shrubs to provide shade can greatly increase the diversity. Limestone areas in subtropical Florida, USA, provide similar habitats and harbor a number of tropical species.

Acknowledgments

Tatiany Oliveira da Silva was my inspiration for this subchapter. She generously gave me her collected papers, her images, her thesis, and her time to review this subchapter. Andi Cairns was helpful in including information about Australia.

Literature Cited

Ah-Peng, C., Chuah-Petiot, M., Descamps-Julien, B., Bardat, J., Stamenoff, P., and Sraberg, D. 2007. Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Réunion. *Divers. Distrib.* 13: 654-662.

- Barthlott, W., Porembski, S., Szarzynski, J., Mund, J. P. 1993. Phytogeography and vegetation of tropical inselbergs. Actes du Colloque International de Phytogéographie Tropicale. Paris, Juin 1993.
- Bastos, C. J. P., Yano, O., and Bôas-Bastos, S. B. V. 2000. Briófitas de campos rupestres da Chapada Diamantina, estado do Bahia, Brasil. Rev. Brasil. Bot. 23: 359-370.
- Benassi, M., Stark, L. R., Brinda, J. C., McLetchie, D. N., Bonine, M., and Mishler, B. D. 2011. Plant size, sex expression and sexual reproduction along an elevation gradient in a desert moss. Bryologist 114: 277-288.
- Bornhardt, W. 1900. Zur Oberflächengestaltung und Geologie Deutsch-Ostafrikas, Vol. 7. Reimer, 40 pp.
- Breen, R. S. 1953. Tropical mosses on limestone. Bryologist 56: 1-7.
- Burke, A. 2002a. Are Namibian inselbergs conservation islands? A floral perspective. S. Afr. J. Sci. 98: 560-562.
- Burke, A. 2002b. Plant communities of a Central Namib inselberg landscape. J. Veg. Sci. 13: 483-492.
- Burke, A. 2003. Floristic relationships between inselbergs and mountain habitats in the central Namib. Dinteria 22: 19-38.
- Conceição, A. A. and Pirani, J. R. 2005. Delimitação de habitats em campos rupestres na Chapada Diamantina, Bahia: Substratos, composição florística e aspectos estruturais. [Delimitation of habitats in rupestrian fields in Chapada Diamantina, Bahia: Substrates, floristic composition and structural aspects.]. Bol. Bot. 23: 85-111.
- Cronberg, N., Natcheva, R., and Hedlund, K. 2006. Microarthropods mediate sperm transfer in mosses. Science 313: 1255.
- Cronberg, N., Natcheva, R., and Berggren, H. 2008. Observations regarding the life cycle of silvermoss *Bryum argenteum*. In: Mohamed, H., Baki, B. B., Nasrullah-Boyce, A., and Lee, P. K. Y. (eds.). Bryology in the New Millennium. University of Malaya, Kuala Lumpur, pp. 347-352.
- During, H. J. and Tooren, B. F. van. 1990. Bryophyte interactions with other plants. Bot. J. Linn. Soc. 104: 79-98.
- Edward, N. and Miller, P. C. 1977. Validation of a model on the effect of tundra vegetation on substrate temperature. Arct. Alp. Res. 9: 89-104.
- Egunyomi, A. 1984. New records for the moss flora of Nigeria. Bryologist 87: 369-370.
- Frahm, J.-P. 1996. Diversity, life strategies, origin and distributions of tropical inselberg bryophytes. An. Inst. Biol. Univ. Nac. Autón. México Ser. Bot. 67: 73-86.
- Frahm, J.-P. 2000. Bryophytes. In: Barthlott, W. and Porembski, S. (eds.). Inselbergs. Ecological Studies 146, Springer Verlag, New York, pp. 91-102.
- Frahm, J.-P. and Porembski, S. 1994. Moose von Inselbergen aus Westafrika. Trop. Bryol. 9: 59-68.
- Frahm, J.-P. and Porembski, S. 1997. Moose von Inselbergen in Benin. Trop. Bryol. 14: 3-9.
- Frahm, J.-P., Porembski, S., Seine, R., and Barthlott, W. 1996. Moose von Inselbergen aus Elfenbeinküste und Zimbabwe. [Mosses from inselbergs of the Ivory Coast and Zimbabwe.]. Nova Hedw. 62: 177-189.
- Frey, W. and Kürschner, H. 2011. Asexual reproduction, habitat colonization and habitat maintenance in bryophytes. Flora – Morphol. Distrib. Funct. Ecol. Plants 206: 173-184.
- Hodgetts, N. G., Matcham, H. W., and Duckett, J. G. 1999. Bryophytes collected in Lesotho, the Natal Drakensberg and the Orange Free State, southern Africa. J. Bryol. 21: 133-155.
- Inuthail, J. and Sridith, K. 2010. The vegetation structure on the granitic inselberg in Songkhla province, Peninsular Thailand. Thailand Forest Bull. (Bot.) 38: 74-89.
- Kürschner, H. 2003. The *Ricciatum jovet-astii-argenteolimbatæ* ass. nov. of the Jabal Arays area, Yemen-life strategies of a remarkable xerotropical African bryophyte community. Nova Hedw. 76: 399-413.
- Kürschner, H. 2006. Syntaxonomy, synecology and life strategies of a saxicolous bryophyte community of Socotra Island, Yemen. Englera 28: 163-174.
- Lüttge, U., Meirelles, S. T., and Mattos, E. A. 2008. Strong quenching of chlorophyll fluorescence in the desiccated state in three poikilohydric and homoiochlorophyllous moss species indicates photo-oxidative protection on highly light-exposed rocks of a tropical inselberg. J. Plant Physiol. 165: 172-181.
- Oyesiku, O. O. 2018. Nutrient uptake of *Archidium acanthophyllum* and *Cyanotis lanata* from savanna microsites on Baasi Inselberg in Southwestern Nigeria. Afr. J. Sci. Nat. in press.
- Oyesiku, O. O. and Amusa, N. A. 2010. *Archidium acanthophyllum* (moss) and *Cyanotis lanata* (Succulent monocot) succession model: Inselberg indicators in Southwestern Nigeria. Arch. Appl. Sci. Res. 2 (6): 1-7.
- Oyesiku, O. O. and Egunyomi, A. 2004. Influence of substrate pH and temperature on association of *Archidium acanthophyllum* (Musci) and *Cyanotis lanata* (Commelinaceae) on Baasi Inselberg SW Nigeria. Afr. J. Ecol. 42: 74-77.
- Peñaloza-Bojacá, G. F., Oliveira, B. A., Araújo, C. A. T., Fantecelle, L. B., and Maciel-Silva, A. S. 2018a. Bryophyte reproduction on ironstone outcrops: Delicate plants in harsh environments. Flora 238: 155-161.
- Peñaloza-Bojacá, G. F., Oliveira, B. A., Araújo, C. A. T., Fantecelle, L. B., Santos, N. D., and Maciel-Silva, A. S. 2018b. Bryophytes on Brazilian ironstone outcrops: Diversity, environmental filtering, and conservation implications. Flora 238: 162-174.
- Pócs, T. 1982. Tropical forest bryophytes. In: Smith, A. J. E. Bryophyte Ecology. Springer, Dordrecht, pp. 59-104.
- Porembski, S. 2007. Tropical inselbergs: Habitat types, adaptive strategies and diversity patterns. Rev. Brasil. Bot. 30: 579-586.
- Porembski, S. and Barthlott, W. 1996. Plant species diversity of west African inselbergs. In: Maesen, L. J. G. van der, Burgt, X. M. van der, and Rooy, M. (eds.). The Biodiversity of African Plants. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 180-187.
- Porembski, S. and Barthlott, W. 2000. Granitic and gneissic outcrops (inselbergs) as centers of diversity for desiccation-tolerant vascular plants. Plant Ecol. 151: 19-28.
- Porembski, W., Barthlott, W., Dörrstock, S., and Biedinger, N. 1994. Vegetation of rock outcrops in Guinea: Granite inselbergs, sandstone table mountains and ferricretes - remarks on species numbers and endemism. Flora 189: 315-326.
- Porembski, S., Siene, R., and Barthlott, W. 1997. Inselberg vegetation and biodiversity of granite outcrops. J. Royal Soc. West. Austral. 80: 193-199.
- Porembski, S., Martinelli, G., Ohlemüller, R., and Barthlott, W. 1998. Diversity and ecology of saxicolous vegetation mats on inselbergs in the Brazilian Atlantic Rainforest. Biodiv. Res. 4: 107-119.
- Pôrto, K. C., Cavalcanti-Silva, I. C., Reis, L. C., and Maciel-Silva, A. S. 2017. Sex ratios and sporophyte production in the

- moss *Bryum argenteum* Hedw. on a rock outcrop, north-eastern Brazil. *J. Bryol.* 39: 194-198.
- Potembski, S. and Barthlott, W. (eds.). 2012. *Inselbergs: Biotic Diversity of Isolated Rock Outcrops in Tropical and Temperate Regions*. Ecological Studies, Springer Verlag, Berlin, Heidelberg, 525 pp.
- Ribeiro, K. T., Medina, B. M. O., and Scarano, F. R. 2007. Species composition and biogeographic relations of the rock outcrop flora on the high plateau of Itatiaia, SE-Brazil. *J. Bot.* 30: 623-639.
- Richardson, J. A. 1958. The effect of temperature on the growth of the plants on pit heaps. *J. Ecol.* 46: 537-546.
- Sarthou, C. and Villiers, J.-F. 1998. Epilithic plant communities on inselbergs in French Guiana. *J. Veg. Sci.* 9: 847-860.
- Sarthou, C., Kouanda-Kiki, C., Vaçulik, A., Mora, P., and Ponge, J.-F. 2009. Successional patterns on tropical inselbergs: A case study on the Nouragues inselberg (French Guiana). *Flora* 204: 396-407.
- Sarthou, C., Pavoine, S., Gasc, J.-P., Massary, J.-C. de, and Ponge, J.-F. 2017. From inselberg to inselberg: Floristic patterns across scales in French Guiana (South America). *Flora* 229: 147-158.
- Shortlidge, E. E., Rosenstiel, T. N., and Eppley, S. M. 2012. Tolerance to environmental desiccation in moss sperm. *New Phytol.* 194: 741-750.
- Silva, J. B. and Germano, S. R. 2013. Bryophytes on rocky outcrops in the caatinga biome: A conservationist perspective. *Acta Bot. Brasil.* 27: 827-835.
- Silva, J. B., Santos, N. D. D., and Pôrto, K. C. 2014a. Beta-diversity: Effect of geographical distance and environmental gradients on the rocky outcrop bryophytes. *Cryptog. Bryol.* 35: 133-163.
- Silva, T. O. 2012. *Riqueza e diversidade de briófitas em afloramentos rochosos do Estado de Pernambuco, Nordeste do Brasil*. [Richness and diversity of bryophytes on rock outcrops in the State of Pernambuco, Northeast Brazil.]. M.S. dissertation, Universidade Federal de Pernambuco, Centro de Ciências Biológicas, Biologia Vegetal, Brazil, 74 pp.
- Silva, T. O., Silva, M. P. P., and Pôrto, K. C. 2014b. Briófitas de afloramentos rochosos do Estado de Pernambuco, Brasil. [Bryophytes on rocky outcrops in Pernambuco State, Brazil.] *Bol. Mus. Biol. Mello Leitão (N. Sér.)* 36: 85-100.
- Söderström, L. 1994. Substrate preference in some forest bryophytes: A quantitative study. *Lindbergia* 18: 98-103.
- Stark, L. R., McLetchie, D. N., Greenwood, J. L., and Eppley, S. M. 2016. Moss antheridia are desiccation tolerant: Rehydration dynamics influence sperm release in *Bryum argenteum*. *Amer. J. Bot.* 103: 856-864.
- Valente, E. B. and Pôrto, K. C. 2006. Briófitas do afloramento rochoso na Serra da Jibóia, município de Santa Teresinha, Bahia, Brasil. [Bryophytes from the rocky outcrop in the Serra da Jibóia, municipality of Santa Teresinha, Bahia, Brazil.]. *Bol. Inst. Bot.* 18: 207-211.
- Watson, W. 1933. The evolutionary aspects of some xerophytic adaptations in the Bryophyta. *Bryologist* 36: 32-34.

CHAPTER 8-13

TROPICS: INTERACTIONS AND ROLES

TABLE OF CONTENTS

Role.....	8-13-2
Effect on Tree Seedlings.....	8-13-4
Bryophyte and Fauna Relationships.....	8-13-4
Arthropods	8-13-5
Vertebrates.....	8-13-7
Reptiles and Amphibians	8-13-7
Rodents	8-13-8
Bryophytes on Fungi.....	8-13-8
Summary.....	8-13-8
Acknowledgments	8-13-9
Literature Cited.....	8-13-8

CHAPTER 8-13

TROPICS: INTERACTIONS AND ROLES



Figure 1. *Craugastor bransfordii* on mosses in the tropics. Note the moss stuck to its skin (arrow). Photo by Jason Folt, with permission.

Role

Although we have discussed the role of bryophytes in retaining water earlier, its role in water relations in the tropics cannot be overemphasized. Romero (1999) suggested that bryophyte sensitivity to moisture could be an indicator of the health of the forests where the bryophytes abound. In one submontane forest in Tanzania, epiphytes (including bryophytes, lichens, and tracheophytes) comprised $2,130 \text{ kg ha}^{-1}$, intercepting about 15,000 L of rainfall water per hectare (Pócs 1980). In the elfin (cloud) forest, at only 2,120 m, a biomass of $14,000 \text{ kg ha}^{-1}$ intercepts nearly 50,000 L ha^{-1} . Thus, the impact of bryophytes on the water and nutrient regime of the cloud forest is surely significant.

In montane forests, bryophytes make considerable contribution to both biomass and litter. Growth of epiphytic bryophytes in Monteverde, Costa Rica, was approximately 39-49.9% per year, providing a net productivity of $122\text{-}203 \text{ g m}^{-2} \text{ yr}^{-1}$ (Clark *et al.* 1998). Nitrogen accumulation in these bryophytes was also

significant at $1.8\text{-}3.0 \text{ g N m}^{-2} \text{ yr}^{-1}$. Most of the decomposition seems to occur the first year, with loss from litterbags in the canopy of $17\pm 2\%$ and $19\pm 2\%$ by the end of the second year. On the ground, losses were quite different, with $29\pm 2\%$ the first year and $45\pm 3\%$ after two years. One advantage to the ecosystem was that approximately 30% of the initial N mass was released rapidly both on the ground and from canopy litter. Furthermore, green shoots on the ground lost about 47% of their initial N content within the first three months. Although these were significant rapid releases from these sources, providing a steady supply of N to the soil, the remaining N content was recalcitrant, creating an N sink within the bryophytes. What may be more important is their role in transforming N from mobile forms reaching the canopy as atmospheric deposits to highly immobile forms. This maintenance of low N levels despite atmospheric deposition may help to maintain these low-nutrient bryophyte habitats and prevent the conversion to graminoids more typical of fertilized soil conditions.

Even in lowland floodplain forests, bryophyte biomass can be significant in the accumulation of nutrient elements. With an accumulation of only 210-1,400 kg ha⁻¹ ash-free dry weight biomass on 10-year-old stakes in a floodplain, Frangi and Lugo (1992) still considered that the bryophytes in these floodplains served as biotic filters of flood waters that could retain nutrients in the terrestrial system.

In Guadeloupe and other tropical locations, nutrients in the canopy, particularly in the upper canopy of the montane rainforest, are released from bryophytes in pulses (Coxson 1991). These pulses result from rewetted bryophytes that have suffered membrane damage during desiccation. The ions are normally those of intracellular pools that were not otherwise available to the throughfall. During rewetting experiments, concentrations reached 11.8 kg ha⁻¹ yr⁻¹ for N, 1.4 kg ha⁻¹ yr⁻¹ for P, and 80.1 kg ha⁻¹ yr⁻¹ for K.

Bryophytes provide a substrate for tracheophyte epiphytes to become established. In a study of the palm *Socratea exorrhiza* (Figure 2), Zotz and Vollrath (2003) found that tracheophytic epiphytes on these trunks are associated with bryophyte patches to a much greater extent than dictated by chance, suggesting a higher success rate, but none seem to require bryophytes for establishment. In the lowland rainforest of Guyana the bryophyte mats and their accumulated debris support different tracheophyte epiphytes in the lower canopy than can be found in the middle and upper canopy branches (ter Steege & Cornelissen 1988).



Figure 2. *Socratea exorrhiza*, a palm on which tracheophytic epiphytes are more frequently associated with bryophytes. Photo by A. Araujo, through Creative Commons.

Bryophytes also moderate the microclimate. Stuntz *et al.* (2002) reported the importance of epiphytes in moderating the climate of the crowns in the rainforest, creating a natural air conditioning. In this case, they were discussing members of the pineapple family, finding that water loss through evaporative drying at microsites adjacent to them is nearly 20% lower than at exposed microsites. They create a habitat that is significantly lower in temperature than sites with no epiphytes in the same tree crown. Hence, these tracheophytic epiphytes create a habitat more hospitable to bryophytes, but it is likely that the bryophytes also contribute to evaporative cooling, thus helping to lower the temperature. These cooler microsites with greater moisture provide suitable habitats for small arthropods.

Tropical ferns are often associated with bryophyte-covered substrates. Carvalho *et al.* (2012) noted that *Cochlidium connellii* (see Figure 4), a fern in the Polypodiaceae, grows among mosses in rocky crevices. *Trichomanes robustum* (Hymenophyllaceae; Figure 3) and *Terpsichore taxifolia* (Polypodiaceae; Figure 5) occur on moss-covered trunks in the upper montane forest in Brazil and other locations in the tropics.



Figure 3. *Trichomanes boschianum*; *Trichomanes robustum* grows among mosses in rock crevices in the tropics. Photo by Robert Klips, with permission.



Figure 4. *Cochlidium serrulatum*; *Cochlidium connellii* grows among mosses in rock crevices in the tropics. Photo by Robbin Moran, with permission.



Figure 5. *Terpsichore asplenifolia*; *Terpsichore taxifolia* grows among mosses in rock crevices in the tropics. Photo by Daniel Tejero, with permission from Robbin Moran.

Effect on Tree Seedlings

One might think that bryophytes would benefit tree seedlings by maintaining moisture, but often they are a detriment. The shade tents in the experiments at the alpine treeline in northern Ecuador did indeed have a greater growth of mosses, indicating greater moisture (Bader *et al.* 2007). But thick mats of mosses can be detrimental. Bader and coworkers found that seedlings of forest trees in the tropics often appeared to have negative growth because the bryophytes, especially mosses, grew up around them. This growth often deprived the seedling leaves of light. Bader and coworkers concluded that the seedlings grew in the mosses because no other substrate was available in the forest and did not appear to be benefitted by them.

Bryophyte and Fauna Relationships

In an Ecuadorian cloud forest (Figure 7), Zitani *et al.* (2018) found annelids, molluscs, crustaceans, millipedes, centipedes, arachnids, and hexapods (and others) among the bryophytes. And of course many birds use bryophytes for making nests, especially the pendent and mat-forming species (Cao & Caihua 1991) (see also Chapter 16). And some rodents occur only in mossy forests (see Chapter 17).

When the new species *Herbertus sendtneri* (Figure 6) was discovered, it displayed swollen tips resembling gynoecia (Gradstein *et al.* 2018). These proved instead to be small, whitish colonies of protozoans that resemble gnathifers, but remain to be identified. These infected

shoot tips failed to develop normally and instead produced branch innovations (1-2) below the swollen tips.



Figure 6. *Herbertus sendtneri*. Photo by Paulo Henrique Silva <siaram.azores.gov.pt>, with online permission.

Zitani *et al.* discovered an arboreal **Onychophoran** (velvet worm; Figure 8), along with a **Lepidopteran** (butterfly or moth) mimic, among the epiphytic bryophyte mats that are up to 10 cm deep in an Ecuadorian cloud forest (Figure 7). **Onychophorans** are highly susceptible to desiccation, so the bryosphere most likely maintains their moisture at a safe level.



Figure 7. Ecuadorian cloud forest. Photo by Arthur Anker, with permission.



Figure 8. **Onychophoran**, a moss inhabitant in the tropics. Photo through Creative Commons.

Insects abound in tropical forests, including those in bryophyte mats (Nadkarni & Longino 1990). Epiphytes can contribute antifeedants that help protect the host. Frahm and Kirchhoff (2002) tested alcoholic extracts from the moss *Neckera crispa* (Figure 9) and the liverwort *Porella obtusata* (Figure 10) on feeding by the slug *Arion lusitanicus* (Figure 11). *Neckera crispa* had only low antifeedant properties at 0.5% or more dry weight. *Porella obtusata*, on the other hand, was moderately effective at concentrations of 0.05%, with total effectiveness at 0.25% of dry weight.



Figure 9. *Neckera crispa*, a moss with weak antifeedant activity on the slug *Arion lusitanicus*. Photo by Jan-Peter Frahm, with permission.



Figure 10. *Porella obtusata*, a moss with antifeedant activity against the slug *Arion lusitanicus*. Photo by Jan-Peter Frahm, with permission.



Figure 11. *Arion lusitanicus*, a slug that is deterred by extracts from *Porella obtusata*. Photo by Håkan Svensson, through Creative Commons.

Most of the animal interactions are discussed in the chapters on interactions in volume 2, but some deserve repetition here for those who want a quick view of their roles in the tropics. In addition to the many bryophytes in the tropics and the many more waiting to be discovered, there are likely many unusual or intimate relationships with insects to be discovered.

Arthropods

Many arthropods live among the epiphytic bryophytes. Yanoviak *et al.* (2004) compared the arthropod assemblages in the vegetative portions vs the humic portions of Neotropical cloud forest epiphyte mats. Many types of arthropods occur among the bryophytes of the Neotropical cloud forests. Bryophytes at different elevations and tree levels provide different conditions for these arthropods and thus increase their diversity in the tropics. Furthermore, the green and brown portions of the bryophytes support different communities, with the green portion containing twice as many individuals and species per gram dry mass compared to the brown portion.

Some species of invertebrates seem to be associated exclusively with bryophytic epiphytes. *Bryospilus repens* (Branchiopoda) has been considered a strictly epiphytic moss inhabitant (Cammaerts & Mertens 1999).

The rainforest brings new meaning to letting moss grow on your feet – or head or back. In the cloud forests of Papua New Guinea, at 2,000-3,000 m asl, one can find mosses (*Daltonia angustifolia*; Figure 12) and liverworts [*Cololejeunea* (Figure 13), *Microlejeunea* (Figure 14), and *Metzgeria* (Figure 15)] on the back of a beetle, a small weevil (Curculionidae) in the genus *Gymnopholus* (Figure 12) (Gressitt *et al.* 1965; Gradstein *et al.* 1984; Gradstein & Equihua 1995). *Daltonia* is not restricted to this weevil, but rather grows on bark and small branches of the montane rainforest where it is able to subsist when it is not being transported around the canopy. Gradstein and coworkers (1984) attribute the ability of *Daltonia* to inhabit the beetle to the ability of this moss to mature quickly and grow where the beetle lives. It is likely that the moss affords camouflage to the beetle. Could it also make the beetle distasteful?



Figure 12. *Daltonia angustifolia* on weevil, *Gymnopholus* sp., in the montane mossy forest of New Guinea. Photo by Robert Gradstein, with permission.

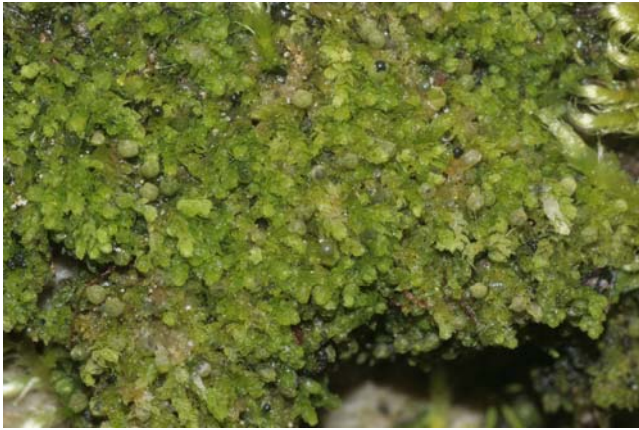


Figure 13. *Cololejeunea calcarea*; members of this genus can inhabit the backs of the weevil *Gymnopholus* sp.. Photo by Hermann Schachner, through Creative Commons.



Figure 14. *Microlejeunea ulicina*; members of this genus can inhabit the backs of the weevil *Gymnopholus* sp. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 15. *Metzgeria claviflora* from the Neotropics; members of this genus can inhabit the backs of the weevil *Gymnopholus* sp. Photo by Michael Lüth, with permission.

Epizoic bryophytes occur on a variety of insects in the tropics. Epiphyllous liverworts sometimes extend their substrate to the forewings and pronotum of the Costa Rican

shield mantids [*Choeradodis rhombicollis* (Figure 16) and *C. rhomboidea* (Figure 17)] (Lücking *et al.* 2010). These insects can become home to five species of liverworts. In their collection of 84 individuals, the researchers found 60 with epiphylls. They colonized more females than males and more of *C. rhombicollis* than *C. rhomboidea*. This is likely due to the longer lifespan of females and suggests that the same should be true for host leaves. The bryophytes may provide camouflage for the insects.



Figure 16. *Choeradodis rhombicollis*, a mantid whose wings can be colonized by epiphyllous liverworts. Photo by Benjamt444, through GNU free documentation license.



Figure 17. *Choeradodis rhomboidea*, a mantid whose wings can be colonized by epiphyllous liverworts. Photo by Andreas Kay, through Creative Commons.

Several mantids and walking sticks are mimics of mosses or liverworts. In other cases, insect larvae may use epiphyllous bryophytes as host plants in the tropics (DeVries 1988).

Callaghan (1992) described the behavior of 16 **Lycaenidae** butterflies in Nigeria. The larvae of all these species grazed on epiphylls "such as lichens and fungi." Mimicry is much more common in the tropics than elsewhere. Occasionally epiphyllous bryophytes, especially liverworts, are able to contribute to this mimicry.

Insects and other animals associated with your bryophyte collections can cause immigration control to quarantine your specimens for months and may result in your never seeing them again. Heating/drying methods beforehand can drive these inhabitants out or kill them, increasing your chances of getting your samples through customs.

Vertebrates

Reptiles and Amphibians

Many tropical amphibians (see, for example, Allison & Kraus 2000) and some snakes and lizards are associated with bryophytes. Many tropical epiphytes provide nesting sites and cover for animals such as salamanders (Bruce 1999). Some amphibians use them as calling sites, with the bryophytes modifying the types of sounds they make. Others use them for egg-laying sites. See Chapters 14 (Amphibians) and 15 (Reptiles) in Volume 2 (Bryological Interaction) for details.

In a study in the montane cloud forest of Cameroon, Böhme and Fischer (2000) found lizards with a greenish coloration. This ground chameleon, *Rhampholeon spectrum* (Figure 18), was sporting an overgrowth of four species of typically epiphyllous liverworts from the family Lejeuneaceae. The species included *Cololejeunea jovetastiana* (see Figure 19) and *Colura digitalis* (Figure 20) as the most abundant; only a few plants of *Cololejeunea* sp. were present; *Lejeunea* (Figure 21) was present in only two samples.



Figure 18. *Rhampholeon spectrum* in Cameroon, a species that can be inhabited by several species of liverworts in the Lejeuneaceae. Photo by Bernard DuPont, through Creative Commons.



Figure 19. *Cololejeunea minutissima*; *Cololejeunea jovetastiana* is one of the leafy liverworts known to live on the lizard *Rhampholeon spectrum*. Photo by David T. Holyoak, with permission.

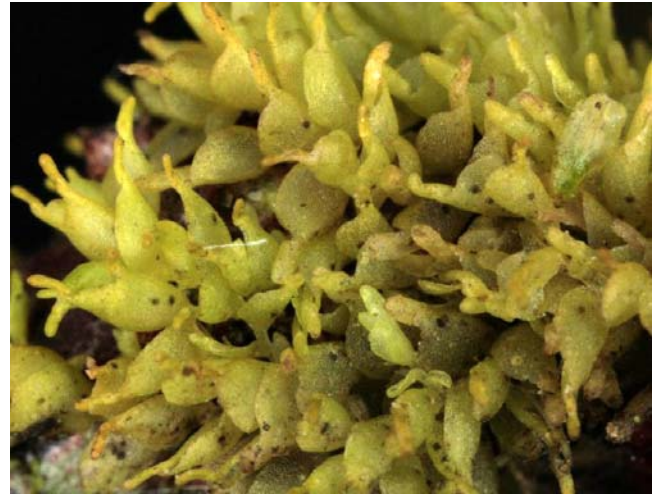


Figure 20. *Colura digitalis*, one of the leafy liverworts known to live on the lizard *Rhampholeon spectrum*. Photo by Jan-Peter Frahm, with permission.



Figure 21. *Lejeunea anisophylla*; *Lejeunea* is one of the genera of leafy liverworts known to live on the lizard *Rhampholeon spectrum*. Photo by Lionel Courmont, through Creative Commons.

But a stranger vision might be that of a lizard with a head dress! In the Mexican rainforest, *Corythophanes cristatus* (Figure 22-Figure 23), a lizard of the lowland rainforest of the Chiapas, sports a crown of filamentous algae including *Cladophora* (dominant; Figure 24), and Chaetophorales (Figure 25), with the tiny leafy liverwort *Taxilejeunea obtusangula* (Figure 26) living among them (Gradstein & Equihua 1995). This liverwort species is normally a common bark inhabitant, but also occurs on rocks (Evans 1911).



Figure 22. *Corythophanes cristatus*, a lizard species that uses its head as a shovel and sometimes carries a mantle of bryophytes there. Photo by Simon J. Tonge, through Creative Commons.



Figure 23. Head of *Corythophanes cristatus* showing colonization by bryophytes. Photo by Twan Leenders, with permission.



Figure 24. *Cladophora* sp., a green alga that lives on the heads of *Corythophanes cristatus*. Photo by Kristian Peters, through Creative Commons.



Figure 25. *Stigeoclonium* sp., an alga in the *Chaetophorales* – an order of green algae known to live on the heads of *Corythophanes cristatus*. Photo by Kristian Peters, through Creative Commons.

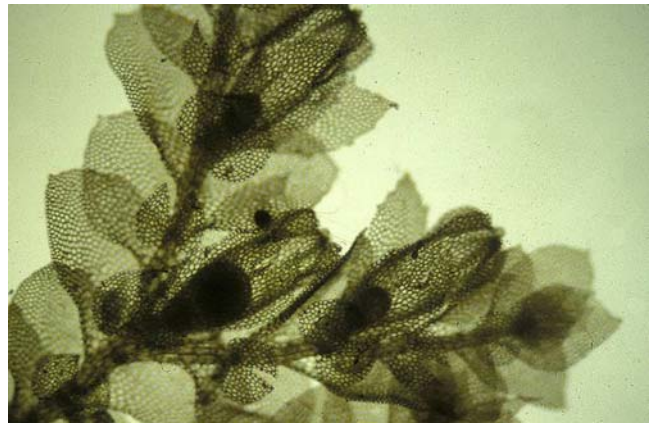


Figure 26. *Taxilejeunea obtusangula*, one of the inhabitants on some crested lizards, *Corythophanes cristatus*. Photo by Elena Reiner-Drehwald, with permission.

Rodents

Even mice (moss mice) live among bryophytes in the tropics. In Sulawesi, Indonesia, moss mice live and nest among the bryophytes (Helgen & Helgen 2009).

Bryophytes on Fungi

A surprising number of bryophytes are able to grow on the sporocarps of *Basidiomycota* fungi. Vital *et al.* (2000) identified 26 moss and 35 liverwort species growing on these substrates. None was exclusive to the fungi, all occurring on dead trunks where fungi occurred as well. Could it be that the fungus provides some chemical that is needed for the bryophyte life cycle to be completed?

Summary

Bryophytes can play major roles in water and nutrient cycling in tropical forests. In particular, they provide suitable habitat for nitrogen-fixing Cyanobacteria, as well as trapping nutrients from rainwater and the atmosphere. These nutrients can be

released in pulses, often at important times for forest growth.

Bryophytes in trees provide suitable substrate for many species of flowering and fern epiphytes, but their exact role is poorly known. On the other hand, many organisms use the mosses as homes or for nesting materials. Inhabitants include insects and other arthropods, velvet worms, annelids, molluscs, frogs, snakes, and rodents. On the other hand, bryophytes can inhibit the growth of bacteria and fungi and discourage herbivory by insects and other herbivores. Some of these organisms are known exclusively from bryophytes. Rodents and birds use bryophytes as nesting materials. Some bryophytes grow on insects or lizards and may provide camouflage. And a surprisingly large number of bryophytes are able to grow on fruiting parts of fungi.

Acknowledgments

My appreciation goes to Sean Edwards, who frequently has sent me interesting publications on interactions of animals and bryophytes.

Literature Cited

- Allison, A. and Kraus, F. 2000. A new species of frog of the genus *Xenorhina* (Anura: Microhylidae) from the north coast ranges of Papua New Guinea. *Herpetologica* 56: 285-294.
- Bader, M. Y., Geloof, I. van, Rietkerk, M. 2007. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. *Plant Ecol.* 191: 33-45.
- Böhme, W. and Fischer, E. 2000. Ein Bodenhamäleon (*Rhampholeon spectrum*) mit Pflanzenbewuchs: Zweiter Nachweis von Moosen auf einem lebenden Wirbeltier. *Herpetofauna* 22: 5-10.
- Bruce, R. C. 1999. Life history attributes of a rare neotropical salamander, *Nototriton picadoi* (Plethodontidae: Bolitoglossini). *Herpetol. Rev.* 30: 76-78.
- Butler, R. A. 2006. Tropical Rainforests of the World. Mongabay.com. Accessed on 5 December 2008 at <<http://rainforests.mongabay.com/0101.htm>>.
- Cachan, P. 1963. Signification ecologique des variations microclimatiques verticales dans le forêt sempervirente de Basse Cote d'Ivoire. *Ann. Fac. Sci. Dakar* 8: 89-155.
- Callaghan, C. J. 1992. Biology of epiphyll feeding butterflies in a Nigerian cola forest (Lycaenidae: Lipteninae). *J. Lepidopt. Soc.* 46: 203-214.
- Cammaerts, E. and Mertens, J. 1999. A new genus and two new species of Chydoridae (Branchiopoda: Anomopoda), from Korup National Park, Cameroon. *Belgian J. Zool.* 129: 327-337.
- Cao, T. and Caihua, G. 1991. First report on bryophyte bird-nests and their bryophytes in China. *Wuyi Sci. J.* 8: 207-213.
- Carvalho, F. A., Salino, A., and Zartman, C. E. 2012. New country and regional records from the Brazilian side of Neblina Massif. *Amer. Fern J.* 102: 228-232.
- Clark, K. L., Nadkarni, N. M., and Gholz, H. L. 1998. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica* 30: 12-23.
- Coxson, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Can. J. Bot.* 69: 2122-2129.
- DeVries, P. 1988. The use of epiphylls as larval hostplants by the tropical rionid butterfly, *Sarota gyas*. *J. Nat. Hist.* 22: 1447-1450.
- Evans, A. W. 1911. The Hepaticae of the Bahama Islands. *Bull. Torrey Bot. Club* 38: 205-222.
- Frahm, J. P. and Kirchhoff, K. 2002. Antifeeding effects of bryophyte extracts from *Neckera crispa* and *Porella obtusata* against the slug *Arion lusitanicus*. *Cryptog. Bryol.* 23: 271-275.
- Frangi, J. L. and Lugo, A. E. 1992. Biomass and nutrient accumulation in ten year old bryophyte communities inside a flood plain in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 24: 106-112.
- Gradstein, S. R. and Equihua, C. 1995. An epizoic bryophyte and algae growing on the lizard *Corythophanes cristatus* in Mexican Rain Forest. *Biotropica* 27: 265-268.
- Gradstein, S. R., Vitt, D. H., and Anderson, R. S. 1984. The epizoic occurrence of *Daltonia angustifolia* (Musci) in Papua New Guinea. *Cryptog. Bryol. Lichénol.* 5: 47-50.
- Gradstein, R., Vanderpoorten, A., Reenen, G. van, and Cleef, A. 2018. Mass occurrence of the liverwort *Herbertus sendtneri* in a glacial lake in the Andes of Colombia. *Rev. Acad. Colomb. Cien. Exact. Físicas Nat.* 42: 221-229.
- Gressitt, J. L., Samuelson, G. A., and Vitt, D. H. 1968. Moss growing on living Papuan moss-forest weevils. *Nature* 217: 765-767.
- Helgen, K. M. and Helgen, L. E. 2009. Chapter 8. Biodiversity and biogeography of the moss-mice of New Guinea: A taxonomic revision of *Pseudohydromys* (Muridae: Murinae). In: Voss, R. S. and Carleton, M. D. (eds.). *Systematic Mammalogy, Contributions in Honor of Guy G. Musser*. *Bull. Amer. Mus. Nat. Hist.* 331: 230-
- Lücking, R., Mata-Lorenzen, J., and Dauphin, L. G. 2010. Epizoic liverworts, lichens and fungi growing on Costa Rican Shield Mantis (Mantodea: Choeradodis). *Studies Neotrop. Fauna Environ.* 45: 175-186.
- Nadkarni, N. M. and Longino, J. T. 1990. Invertebrates in canopy and ground organic matter in a neotropical montane forest, Costa Rica. *Biotropica* 22: 286-289.
- Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rain forest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Scient. Hung.* 26: 143-167.
- Romero, C. 1999. Reduced-impact logging effects on commercial non-vascular pendant epiphyte biomass in a tropical montane forest in Costa Rica. *Forest Ecol. Mgmt.* 118: 117-125.
- Steege, H. ter and Cornelissen, J. H. C. 1988. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. *Biotropica* 21: 331-339.
- Stuntz, S., Simon, U., and Zotz, G. 2002. Rain forest air-conditioning: The moderating influence of epiphytes on the microclimate in tropical tree crowns. *Internat. J. Biometeor.* 46: 53-59.
- Yanoviak, S. P., Walker, H. A., and Nadkarni, N. M. 2004. Arthropod assemblages in vegetative vs. humic portions of epiphyte mats in a Neotropical cloud forest. *Pedobiologia* 48: 51-58.
- Zitani, N. M., Thorn, R. G., Hoyle, M., Schulz, J. M., Steipe, T., Ruiz, Y. B., Sarquis-Adamson, Y., and Wishart, A. E. 2018. An Onychophoran and its putative Lepidopteran mimic in

the arboreal bryosphere of an Ecuadorian cloud forest.
Amer. Entomol. 64: 94-101.

Zotz, G. and Vollrath, B. 2003. The epiphyte vegetation of the palm *Socratea exorrhiza* – Correlations with tree size, tree age and bryophyte cover. J. Trop. Ecol. 19: 81-90.

CHAPTER 8-14

TROPICS: DISTURBANCE AND CONSERVATION

TABLE OF CONTENTS

Natural Disturbance	8-14-2
El Niño and Hurricanes.....	8-14-2
Nutrient Relationships	8-14-3
Recovery	8-14-3
Bryophyte Loss Effect on Tracheophytes	8-14-4
Fire.....	8-14-5
Volcanoes.....	8-14-5
Animal Activity	8-14-6
Rare and Threatened Species	8-14-7
Pollution and Disturbance	8-14-8
Deforestation.....	8-14-9
Fragmentation Effects.....	8-14-16
Harvesting.....	8-14-17
Industrialization and Air Pollution.....	8-14-19
Radiation.....	8-14-21
Man-made Habitats	8-14-22
Climate Change.....	8-14-24
Recovery	8-14-24
Conservation Issues.....	8-14-26
Current Status.....	8-14-29
Summary	8-14-30
Acknowledgments.....	8-14-30
Literature Cited	8-14-30

CHAPTER 8-14

TROPICS: DISTURBANCE AND CONSERVATION



Figure 1. Deforestation in Indonesia, a common scene throughout the tropics. Photo from Rainforest Action Network, through Creative Commons.

From a northern perspective, most of what we hear about the tropics is about massive disturbance. Hence, it would be irresponsible to discuss this region without at least a glimpse of the impact of disturbance on the bryophyte flora. Unfortunately, we have no before-and-after data for the vast areas that have been converted from tropical rainforest into short-lived agricultural land and that are now experiencing the jungle of plants tolerant of low nutrients, shallow soil, and exposure. However, some recent comparative studies may help us understand what we have lost.

Natural Disturbance

Nature has her own form of devastating disturbances. These include events such as hurricanes, tornadoes, and other high winds, animal activities, volcanoes, fire, and extreme drought.

El Niño and Hurricanes

Despite the frequency of hurricanes in some tropical areas, it appears that few studies have addressed the effects

on bryophyte communities. Weber (1985) seems to be one of the earliest. He assessed the effects on both bryophytes and lichens resulting from the El Niño in the Galápagos Islands.

Hurricanes can have severe impacts on the epiphytic bryophytes in the tropics (Loope *et al.* 1994). Hurricanes can be very powerful forces that destroy nearly everything in their paths. In Puerto Rico, Hurricane Hugo created mass destruction in 1989. Recovery in the cool cloud forest has been slow compared to that of the lowland. Bryophytes were stripped from the trees by the high-powered winds and rain. Fortunately, the return frequency of hurricanes to any given area is low, usually occurring after years or decades (Lodge & McDowell 1991). But at the same time, the life span of a canopy tree or a forest ecosystem is longer than that interval.

Considering the number of hurricanes in the tropics, and the considerable damage I have witnessed to epiphytic bryophyte communities following Hurricane Hugo (Weaver 1999) in Puerto Rico, I am surprised at how few

studies have addressed the damaging effects of hurricanes on these communities.

Nutrient Relationships

Nutrient levels can affect the damage to trees and their adhering bryophytes. Herbert *et al.* (1999) found that large trees sustained damage at twice the frequency of smaller trees. Thus, trees that had a richer phosphorus environment were more susceptible to damage due to greater growth.

Hurricanes alter the nutrient cycling in tropical forests (Lodge *et al.* 1991). Hurricane Hugo (Figure 2), in September 1989, struck Puerto Rico, severely damaging wet forest sites. This, and other hurricanes since, have caused a massive increase in fine litter as leaves (Figure 3), small twigs, and other miscellaneous debris were ripped from the trees and deposited on the forest floor. Concentrations of N and P increased as much as 1.5 times for N and 3.3 for P compared to normal litter fall. This raises the question of effects on competition and the success of bryophytes under these conditions.



Figure 2. Hurricane Hugo forest damage in Puerto Rico. Photo by Matthew C. Larsen and Angel J. Torres Sánchez, USGS, through public domain.



Figure 3. El Yunque forest after Hurricane Irma, showing extensive leaf litter and branches brought down by the hurricane. Photo by Joel S. Olivencia, USDA, through public domain.

Walker *et al.* (1996) mentioned bryophytes in their study comparing altitudinal responses by hurricane-damaged forests in Puerto Rico. Nutrient treatments initiated 1-6 months after the hurricane decreased the bryophytes threefold while causing graminoids to increase 10-fold in the cloud forest (Walker *et al.* 1996).

The cloud forest understory is dominated by bryophytes; epiphytes are common. Walker *et al.* (1996) tested the effects of fertilization on the vegetation following hurricane damage. Fertilization increased biomass of the graminoids (grasses, sedges) in the elfin cloud forest by a factor of 10, whereas bryophytes decreased 3-fold. The same differences were absent in the lowland forest. Cover of ferns did not respond to differences in treatment or time. At the high elevations, bryophyte biomass is most likely sustained by the constant high humidity. It is likely that the bryophytes were negatively affected by the fertilizer salts. They could also have been out-competed by the graminoids. Recovery of the bryophytes was most likely facilitated by their ability to spread. As I have observed in Puerto Rico after Hurricane Hugo (Figure 2), the bryophytes are removed from the trees in patches, leaving behind the source for new growth. This removal is due to high winds and driving rain.

Recovery

Some bryophytes escape damage by living in protected locations. The rare liverwort species *Lejeunea paucidentata* (Lejeuneaceae; Figure 4) occurs in the rainforests of Dominica (Figure 5) (Schäfer-Verwimp 1999). Fortunately, it escapes hurricane damage because it lives on small fern fronds in the undergrowth and benefits from similar conditions in humid secondary vegetation or in heavily damaged old growth rainforest. On the other hand, Schäfer-Verwimp considers that the disappearance of *Phycolepidozia exigua* (Figure 6) is possibly due to hurricane damage to bark. This species most commonly grows on the bark of old trees, but old trees tend to be more susceptible to hurricane damage than the more pliable young trees.



Figure 4. *Lejeunea paucidentata* with perianths and young sporophytes. Photo by Elena Reiner-Drehwald, with permission.

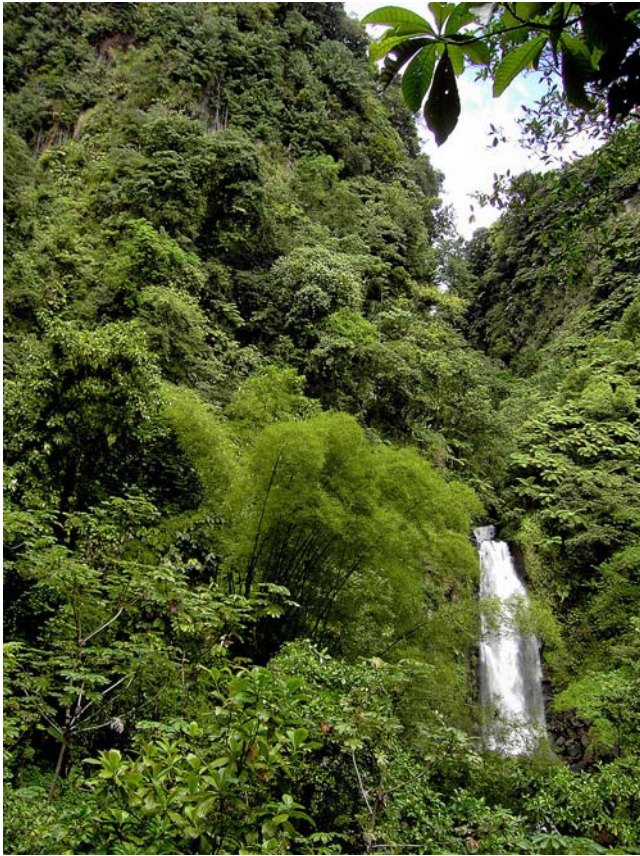


Figure 5. Rainforest at Trafalgar Falls, Dominica. Photo by Hans Hillewaert, through Creative Commons.

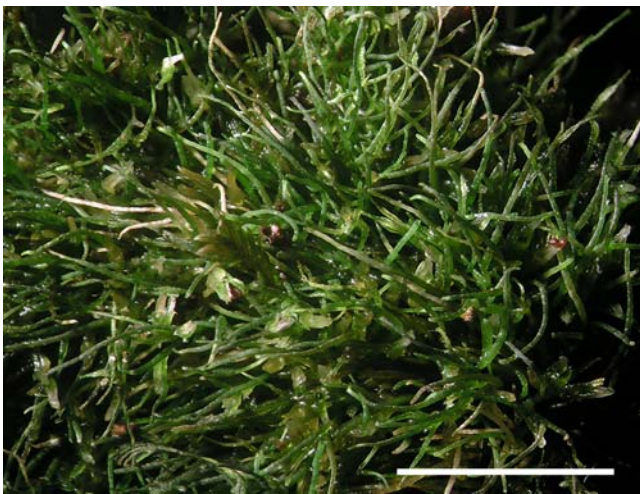


Figure 6. *Phycolepidozia indica*, a species that seems to have disappeared due to hurricanes. Photo by Uwe Schwarz, courtesy of Robbert Gradstein.

Many have tried to determine what limits the species that become established on a given tree. Yeaton and Gladstone (1982) tried to determine what determines the structure of the tracheophytic epiphyte community on the calabash tree (*Crescentia alata*; Figure 7-Figure 8). As a result of their data analysis, they hypothesized that the colonization pattern is the result of the quantity of propagules produced by each species. It is possible that this is an important factor for bryophytes as well.



Figure 7. *Crescentia alata* with epiphytes in the Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.



Figure 8. *Crescentia alata* in the Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Nadkarni (2000) found a 30% reduction in bryophyte cover at severely impacted sites. She demonstrated, by experimental branch stripping, that epiphyte colonization occurs upwards from the **abaxial** (in this case, lower) branch surface. She considered that the shading by the branch permitted these abaxial sites to retain more water, increasing the time that the surface provided a suitable microclimate.

Bryophyte Loss Effect on Tracheophytes

Batke and Kelly (2015) documented the effects of a hurricane on the epiphytic bryophytes in the Cusuco National Park, northwest Honduras (Figure 9). They considered the epiphytes to be mechanically dependent plants and examined how hurricanes affected these dependents (Figure 10). Although the effect on bryophytes was not discussed directly, the researchers found that differences in life forms and families of tracheophytes among the tree branches resulted from branch surface area and bryophyte cover. Hence, the destruction of bryophyte mats led to reduced communities of tracheophytic epiphytes. They found that branches on trees that were more severely impacted had significantly lower cover. They considered that branches that were stripped of bryophytes and their dependent (Figure 10) plants during the severe gusts are less likely to experience early recolonization.



Figure 9. Cusuco National Park, Honduras. Photo by Anjelkaido, through public domain.



Figure 10. Montaña de Yoro forest in Honduras, showing the numerous epiphytes. Photo by Josiah Townsend, with permission.

Damage to the bryophyte communities can affect other epiphytes as well. Tremblay (2008) assessed the relationships of a rare epiphytic orchid after Hurricane Georges. At first he could find no correlation with the percent cover of mosses on standing trees. But a non-parametric density contour map revealed that the moss density does seem to affect the population size of the orchids. Using this technique, Tremblay demonstrated that the orchids are present more frequently when there is a 40-90% moss cover.

Fire

Many forests around the world are subject to fire. In the tropical cloud forests, the bryophytes may actually reduce fire damage. They not only reduce the likelihood of fire because of the moisture they hold, they also facilitate growth of additional epiphytes through their moisture-absorbing and moisture-holding capacity (Proctor 1982; Frahm & Gradstein 1991). This moisture-holding capacity reduces the flammability of the forest (Brujinzeel & Proctor 1995).

Nepstad *et al.* (2008) noted that forest degradation and dieback and subsequent drought increase the susceptibility to forest fires. And fires increase drought, further increasing the susceptibility to bryophyte loss. Furthermore, deforestation and smoke can inhibit rainfall, further increasing fire risk. These researchers predicted

that in the next 20 years following 2008 approximately 55% of the Amazon forests will be cleared, logged, damaged by drought, or burned.

Diaspore banks can facilitate recovery of bryophytes after a fire. In a diaspore bank, Zander and During (1999) found the moss *Neophoenix matoposensis* (Pottiaceae) in Zimbabwe as a new species. They recommended the "forced diaspore bank analysis" as a means to find small species with short life cycles, giving them only limited above-ground exposure. In this case the method was used to uncover species in experimental fire plots. Two additional species were uncovered as new to Zimbabwe and new to Africa. One of these was previously known only from Brazil and Australia.

Volcanoes

Air pollution is not always of human origin. Volcanic activity (Figure 11, Figure 15) can be a major contributor. Baudoin (1985) reported that epiphyllous bryophytes can be used satisfactorily as indicators of volcanic air pollution.



Figure 11. Pāhoehoe lava flows, Hawaii. Picture from Brocken Inaglory, through Creative Commons.

Volcanoes offer opportunities for observing effects of elevation with fewer environmental variables than most substrates. However, when they erupt, they create severe disturbances. These severe habitats, following cooling, create bare rock substrate that differs drastically from the surrounding area. Smith (1981) compared the bryophyte and lichen communities of these severe substrates with those of the surrounding ecosystems at the Puhima Geothermal Area in the Hawaii Volcanoes National park. He found very few of the species from surrounding areas to be present on the volcano ground in geothermal areas. The center of the geothermal area is nearly lacking in any vegetation. Only small communities of vegetation, dominated by the endemic moss *Campylopus praemorsus* (see Figure 12) are scattered here. The mosses seem to provide a safe haven for the lichen *Cladonia oceanica* (see Figure 13), where it grows epiphytically on the mosses in areas lacking the high temperatures. Outside that central zone, where temperatures are lower, the grass *Andropogon* (Figure 14) dominates. Here, both *Campylopus praemorsus* and *Cladonia oceanica* commonly produce reproductive structures.



Figure 12. *Campylopus holomitrius* in a geothermal area; *Campylopus praemorsus* occurs in volcanic and geothermal areas of Hawaii. Photo by Janice Glime.



Figure 13. *Cladonia* sp.; *Cladonia oceanica* is a geothermal lichen that grows epiphytically on the mosses. Photo by Tigerente, through Creative Commons.



Figure 14. *Andropogon leucostachyus*; the genus *Andropogon* dominates outside that central zone of a geothermal vent, where temperatures are lower. Photo by João Medeiros, through Creative Commons.

In Costa Rica, Griffin (1974) suggested that sulfur gasses downwind from a volcano might account for the paucity of mosses there. Both species composition and cover of mosses are diminished on the downwind side of the Poas Volcano (Figure 15).



Figure 15. Poas Volcano, Costa Rica, showing downwind plume of steam. Photo by Franz Xaver, through Creative Commons.

Ah-Peng *et al.* (2007) found 70 species of bryophytes on a 19-year-old lava flow. They suggested that the high diversity is promoted by the host substrate and the bryophyte adaptations to colonize this new substrate. Hence, the disturbance by the volcano brought new space there to house a wide diversity of pioneer organisms.

Animal Activity

Forest animals can likewise be very destructive to bryophytes (Nadkarni 2000). Howler monkeys (*Alouatta* spp.; Figure 16) and tayras (*Eira barbara*; Figure 17) knock clumps of moss and other epiphytes from the branches as they climb and jump about. White-faced capuchins (*Cebus capucinus*; Figure 18) remove them to look for invertebrates in the bromeliads. Most literature indicates that such disturbances are easily and quickly healed with recolonization coming primarily through encroachment from the sides of the plots, thus having the same species. But in the detailed study at Monteverde, Costa Rica, mimicking effects of animal activity, Nadkarni found something quite different when she removed 75 cm strips of epiphytes from canopy branches. Despite the presence of neighboring plants, recolonization was extremely slow, with no colonization during the first five years after stripping. When it did occur, the communities were quite different. Crustose and foliose lichens began the colonization, two groups that were totally absent originally. And rather than encroaching from the sides, colonization extended from the bottoms of the branches. By the sixth year, there were some algae and bryophytes on the undersides of branches. It was not until the eighth year that some of the bryophytes from the underside had joined on the top side. Small seedlings began to appear in the tenth year.



Figure 16. *Alouatta palliata* (Howler Monkey), an animal whose activities in the trees can dislodge clumps of bryophytes. Photo by Hans Hillewaert, through Creative Commons.



Figure 17. Tayra, an animal whose activities in the trees can dislodge clumps of bryophytes. Photo by Greg Hume, through Creative Commons.



Figure 18. White-faced Capuchin (*Cebus capucinus*) in Costa Rica, a species that removes mosses in search of invertebrates. Photo by Cephas, through Creative Commons.

Rare and Threatened Species

By their very nature, severe habitats often have rare and endangered species. That is because bryophytes must have special adaptations to survive in these extreme habitats. Perhaps they sacrifice competitive ability to achieve this physiological adaptation.

Gradstein (1992a) noted that loss of tropical species may vary considerably in deforested areas, depending on the size of the area affected and degree of habitat change. This damage is greatest for shade epiphytes, with an estimated 10% of rainforest species under threat by 1992. Gradstein listed 19 endangered species and 27 rare ones that are disappearing from the rainforests. Costa Rica and Panama have been particularly vulnerable, along with the Greater Antilles, the Chocó, southeastern Brazil, and parts of Amazonia.

Koponen (1992) considered the bryophytes in the tropical (and temperate) regions to have much more danger of becoming rare or extinct than those of the boreal and Arctic regions. The richest tropical floras are in the rainforests and montane forests, and deforestation creates disjunct patterns. Deforestation is particularly problematic in China, where nearly all the forests have been cut for agriculture. Very few bryophyte species from virgin tropical forests are able to survive in manmade habitats.

On the other hand, some disturbed habitats, created by agroforestry, can provide the conditions needed for some of the rare species. For example, Gradstein (1999) rediscovered the endangered leafy liverwort *Sprutheanthus theobromae* (Lejeuneaceae; Figure 19) on cacao trees (*Theobroma cacao* (Figure 20) in western Ecuador.



Figure 19. *Spruceanthus theobromae*, a species endemic to cacao plantations. Photo by Robbert Gradstein, with permission.



Figure 20. *Theobroma cacao* with bryophytes; this species supports some forest bryophytes in plantations in the tropics. Photo by Fpalli, through Creative Commons.

The real loss of tropical rare and endangered species is difficult to assess. Many areas were destroyed before any bryophyte assessment occurred. And many species considered rare or endemic have proven to be synonyms of species in a neighboring country or mountain.

Pollution and Disturbance

Managing for bryophytes often does not coincide with the best management plan for the forest. Andersson and Gradstein (2005) studied the biodiversity of bryophyte and

lichen epiphytes in cacao plantations (Figure 21) in western Ecuador. They found 51 bryophyte and 61 lichen species. The managed cacao plantation epiphyte assemblages resembled those of natural tropical rainforests, but with lower species richness. Species also were typically found lower on the trunks. The species on cacao were typically widespread Neotropical or pantropical species. But *Spruceanthus theobromae* (Figure 19) is endemic to cacao plantations in western Ecuador. Management involving manual removal of epiphytes in the plantations significantly impacted the epiphyte species diversity. High management intensity particularly affected diversity of liverworts and lichens, but not mosses. As one might expect, plantations with low management had the highest percent cover of bryophytes. Plantations with low and moderate management serve as reserves for some ecological specialists, making them important in the conservation of epiphytes.



Figure 21. *Theobroma cacao* plantation in Dominican Republic, home for a number of bryophytes, some of which would normally be in local forests. Photo by C. T. Cooper, through public domain.

Working in tropical rainforests of the Pacific, Pócs and Tóthmérész (1997) found that the average species richness in the most diverse epiphyll communities was 8-9 per leaf. Degraded habitats exhibited as few as 3-4 species. At the habitat level, the number of species could reach 24-25 species. The number of species per habitat does not typically decrease as a result of habitat degradation because **beta diversity** (differences in species composition among sites; regional diversity) tends to increase while the number of species per leaf decreases. The study emphasizes the importance of the scale of the study in order to assess the impacts of disturbance.

Some of our understanding of microhabitat differences can be derived from studies on the effects of disturbance. For example, Werner and Gradstein (2009) compared various degrees of disturbance in closed-canopy mixed acacia forest (old secondary), pure acacia forest (old secondary), forest edge, young semi-closed secondary woodland, and isolated trees in grassland. They found that density of bryophytic epiphytes on 100 trees of *Acacia macracantha* (Figure 22) in northern Ecuador at 2,300 m asl is significantly lower in edge habitat and on isolated trees than in closed forest. Forest edge is more

impoverished than semi-closed woodland and has similar floristic affinity to isolated trees and to closed forest types. The microhabitats among these habitat types vary, contributing to the diversity. As they point out, "Assemblages were significantly nested; habitat types with major disturbance held only subsets of the closed forest assemblages, indicating a gradual reduction in niche availability." They found no diversity effect from distance to the forest for epiphytes on isolated trees. Species density is closely correlated with crown closure. They concluded that microclimate, not dispersal constraints, determine most of the epiphyte assemblage. The researchers also concluded that the bryophytic epiphytes are sensitive indicators of changes in microclimate and human disturbance in the montane dry forests. A major treatise on the canopy community is that of Lowman *et al.* (2013).



Figure 22. *Acacia macracantha*, a species where density of bryophytic epiphytes in northern Ecuador at 2300 m asl is significantly lower in edge habitat and on isolated trees than in closed forest. Photo by Vladeq, through Creative Commons.

Deforestation

Deforestation has become a major factor impacting diversity and biomass in the tropics (Figure 23). "Between 1990 and 1997, 5.8 ± 1.4 million hectares of humid tropical forest were lost each year, with a further 2.3 ± 0.7 million hectares of forest visibly degraded." (Achard *et al.* 2002) although the rate has slowed in recent years, deforestation continues, increasing the total impact.

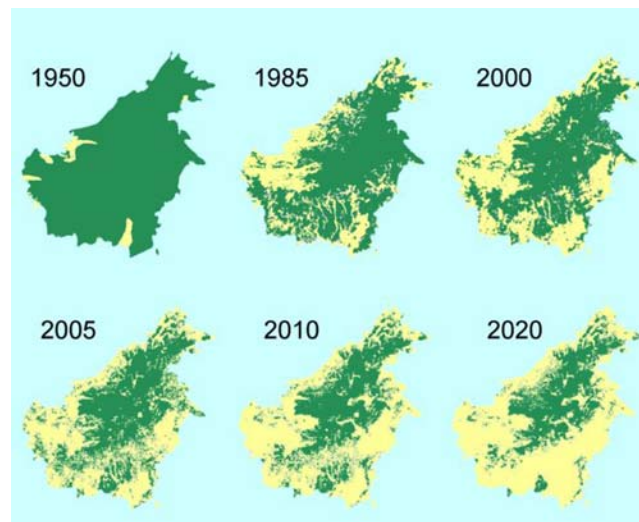


Figure 23. 70 years of Borneo deforestation. Photo courtesy of Robert Gradstein.

Scatena *et al.* (2010) noted that the cloudy, wet, difficult terrain of the tropical montane cloud forests had afforded the bryophytes some protection from deforestation. However, in the late 1970's and early 1980's, even these forests were being torn down or fragmented. By the 1990's they became one of the most threatened ecosystems in the world, with a loss rate exceeding that of the lowland tropical forests ($1.1\% \text{ y}^{-1}$ vs. $0.8\% \text{ y}^{-1}$).

Costa (1999) compared epiphytic bryophyte diversity in primary and secondary lowland rainforests of southeastern Brazil. The highest species richness occurs in mature secondary hillside rainforest (43 species). The lowest is in a highly degraded hillside rainforest (6 species) and a hillside secondary rainforest (5 species). As seen elsewhere, the important families are **Lejeuneaceae** (Figure 4; 23 species, 30%) and **Sematophyllaceae** (Figure 24; 7 species, 10%). And as in other studies, the canopy has the highest number of exclusive species (45% of canopy species). The shade epiphytes are the most affected by deforestation and many do not return 20-45 years after the destruction. However, after 80 years the species composition is similar to that of the primary forest.



Figure 24. *Sematophyllum* (Sematophyllaceae); **Sematophyllaceae** is among the important families from the lowland rainforests of southwestern Brazil. Photo by Michael Lüth, with permission.

In a different location in southeastern Brazil, Costa (1998) found the highest species richness in the mature secondary hillside rainforest (43 species). The lowest is again the highly degraded hillside rainforest (6 species).

Hyvönen *et al.* (1987), however, found that many mosses can find suitable niches even in disturbed areas, unless destruction of the habitat is complete. Nevertheless, some are eliminated by current practices of land use. In their study on the Huon Peninsula of Papua New Guinea, they used 18,000 specimens to determine effects of disturbance on the bryophytes. Of 43 species, 14 were restricted to undisturbed habitats, 16 occurred about equally in both, and 23 were preferentially in disturbed areas. Primeval habitats were dominated by terrestrial & epiphytic mosses; weedy species occurred in disturbed habitats. The sensitive epiphytic species that decreased with disturbance include *Meteorium buchananii* (Figure 25), *Trachypus bicolor* (Figure 26), *T. humilis* (Figure 27), *Pseudotrachypus wallichii*, *Cryptopapillaria fuscescens*, and *Pelekium contortulum* (Figure 28). In addition, *Campylopus clemensiae* (see Figure 39) and *Leptocladia flagellaris* grow on living trees as well as rotten wood. Soil species that are sensitive include *Dawsonia grandis*, *D. papuana* (see Figure 29), *Rhodobryum giganteum* (Figure 30), with less substrate-discriminating *Macrothamnium hylocomioides* (see Figure 31), *Thuidium cymbifolium* (Figure 32), and *T. glaucinum* (Figure 33). Persistent species include *Bryum apiculatum* (Figure 34) and *Plagiomnium integrum* (see Figure 35), although they decrease in altered habitats. On the other hand, the outer crown epiphyte *Leptostomum intermedium* (see Figure 36) seems to increase with human influence, but that could be an artifact due to the difficulty of sampling it. The species that clearly increase with disturbance include *Brachymerium nepalense* (Figure 37), *Bryum billardieri* (Figure 38), *Campylopus exasperatus*, *C. umbellatus* (Figure 39), *Elmeriobryum philippinense*, and *Orthomnion elimbatum* (Figure 40). Species that were clearly present only following disturbance include *Bryum argenteum* (Figure 41) and *B. microerythrocarpum* (= *B. dichotomum*, *B. subapiculum*, or *Gemmabryum subapiculatum*; Figure 42).



Figure 25. *Meteorium buchananii*, a sensitive moss species that decreases with disturbance. Photo by Li Zhang, with permission.



Figure 26. *Trachypus bicolor*, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.



Figure 27. *Trachypus humilis* with capsules, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.



Figure 28. *Pelekium contortulum*, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.



Figure 29. *Dawsonia superba*; *Dawsonia grandis* and *D. papuana* are soil species that are sensitive to disturbance. Photo by Phil Bendle, with permission from John Grehan.



Figure 30. *Rhodobryum giganteum*, a sensitive moss species that decreases with disturbance. Photo by Leonardo L. Co, with online permission.



Figure 31. *Macrothamnium submacrocarpum* from Doi Inthanon, Thailand; *Macrothamnium hylocomioides* is a sensitive soil species that decreases when faced with disturbance. Photo courtesy of Hiroyuki Akiyama.



Figure 32. *Thuidium cymbifolium* with capsules, a sensitive species of soil and other substrates that decreases when faced with disturbance. Photo by Li Zhang, with permission.

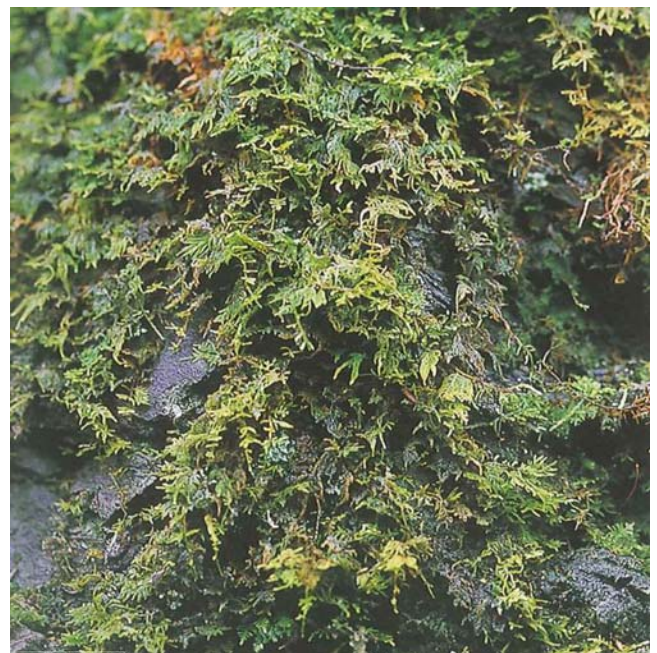


Figure 33. *Thuidium glaucinum*, a sensitive species of soil and other substrates that decreases when faced with disturbance. Photo through Creative Commons.



Figure 34. *Bryum apiculatum* with capsules, a persistent tropical soil species that is less negatively affected by disturbance. Photo by David T. Holyoak, with permission.



Figure 37. *Brachymenium nepalense*, a species that becomes more abundant with disturbance. Photo by Li Zhang, with permission.



Figure 35. *Plagiomnium affine*; *Plagiomnium integrum* is a persistent tropical soil species that is less negatively affected by disturbance. Photo by Michael Lüth, with permission.



Figure 38. *Bryum billardieri*, a species that becomes more abundant with disturbance. Photo by Bramadi Arya, through Creative Commons.



Figure 36. *Leptostomum inclinens* with capsules; *Leptostomum intermedium* is an outer crown species that actually increases with human disturbance. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 39. *Campylopus umbellatus* with capsules, a species that becomes more abundant with disturbance. Photo by Li Zhang, with permission.



Figure 40. *Orthomnion elimbatum*, a species that becomes more abundant with disturbance. Photo by Andrew Franks, with permission.



Figure 41. *Bryum argenteum*, a species that becomes more abundant with disturbance. Photo by Michael Becker, through Creative Commons.



Figure 42. *Bryum microerythrocarpum*, a species that becomes more abundant with disturbance. Photo by Michael Lüth, with permission.

Evidence shows that logging does not have to be totally destructive. The main effect of such disturbance in tropical forests is increased desiccation due to greater wind

movement and insolation, causing a reduction in biomass of epiphytic bryophytes (Norris 1990). This, in turn, decreases the water and mineral retention of the remaining bryophytes and interferes with their ability to trap and release water and mineral nutrients. In Papua New Guinea, Norris found that logging and agricultural practices may alter bryophyte species frequency, but with careful attention to logging management, there is no evidence of a significant loss of species.

When Romero (1999) compared bryophytes in logged and non-logged plots in a tropical montane forest in Costa Rica, he found that pendent epiphytes were more abundant on branches less than 1 cm in diameter. The highest biomass was that of branches supporting shade-tolerant species, *i.e.*, non-logged plots.

A comparison of fallow land (4-15 years) vs submontane rainforest in Bolivia reveals considerably less diversity of both bryophyte families and species in the fallows (Acebey *et al.* 2003). Surprisingly, there is little difference in liverwort diversity between them except in the very young (4-year-old) fallows. Life forms differ, with significantly more smooth mats (72%) in the fallows. Nevertheless, in just 10-15 years, approximately half of the bryophyte taxa of the rainforest are re-established among the trees of the fallows. Most of these arrivals are ecological generalists and sun-loving epiphytes, with ecological specialists and shade species arriving and establishing more slowly. The highest diversity of the fallows is in the understory, contrasting with the highest richness in the canopy of the uncut rainforest. The shift to lower parts of the trees in the fallows corresponds with the greater air humidity there and most likely also with lower temperatures and reduced light intensity.

Return of bryophytes to remnant forests after logging is slow. In subtropical rainforests of Australia, few bryophytes had returned even 25 years after the disturbance (Chapman & King 1983). The same was true in southeastern Brazil (Costa 1999). In Costa Rica, isolated remnant trees (*e.g.* Figure 43), lacking the dense canopy of the undisturbed forest, had bryophyte diversity reduced by 50% compared to the remaining intact forest.



Figure 43. Tropical montane meadow with remnant tree; undisturbed forest is on the far side of the river in back, San Francisco Reserve, Ecuador, 2000 m asl. Photo courtesy of Robert Gradstein.

Much of the land in the tropics has been lost to agriculture before we have even assessed what bryophyte species live there. Sulawesi, Indonesia (Figure 44), is characterized by steep slopes that are often difficult for bryologists to navigate, but logging has nevertheless altered the environment. Ariyanti *et al.* (2008) investigated the bryophytes on tree trunk bases in the natural forest, selectively logged forest, and cacao plantation (Figure 21) shaded by remnants of the natural forest there. They found that species richness differs little among these forest types. But on close inspection, one finds that the moss richness is lowest in the cacao plantations, but the liverwort richness differs little among the forests. By contrast, the moss cover differs little among the forests, but liverwort cover is significantly less in the disturbed forest. Species composition likewise differs markedly in the cacao plantations compared to the natural forests and selectively logged forests. Drought-sensitive species are notably rare or absent in the cacao plantation, with drought-tolerant species replacing them. Large vs small trees have little effect on bryophyte species composition except in the cacao plantation; the latter phenomenon the researchers attribute to changes in stemflow of precipitation water.



Figure 44. Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.

Gradstein and Sporn (2010) compared epiphytic bryophytes from different land use types in several countries of the Neotropics and Indonesia (Sulawesi), including natural rainforests, secondary rainforests, fallows, isolated pasture trees (Figure 20), and cacao agroforests (Figure 21). They found changes in species richness between these disturbed habitats and the various disturbances to vary by 0-10% species loss in the old secondary forest and up to 65-80% loss in young fallows and cacao agroforests. The cacao agroforests lost 75% of their species. In contrast, the remnant forest trees in pastures provide a rich habitat where bryophytes can be conserved. In submontane forests, there were considerable changes in life forms, but these changed little in the montane zones. Sun epiphytes replace shade epiphytes in the deforested areas. The study demonstrates the importance of canopy cover in preserving the rainforest bryophyte vegetation.

Nöske *et al.* (2008) compared the epiphyte diversity of mature and recovering forest and that in open vegetation in the montane zone of Ecuador. They were unable to discern any pattern of change in species richness among different taxonomic groups (lichens, bryophytes, tracheophytes, and moths) with increasing disturbance. However, richness of epiphytic bryophytes decreased significantly from mature forest through the cline to open vegetation. For some of the taxa, the modified habitats serve to increase overall biodiversity in the Andes.

Benítez *et al.* (2015) likewise noted the decline of bryophyte and lichen epiphytes in moist tropical montane forests, due to deforestation and habitat loss. Benítez and coworkers investigated 240 trees in primary and secondary forests of southern Ecuador and found that diversity is higher in primary forests and lower in monospecific secondary forest stands. Habitat loss and reduction of canopy cover negatively affect total diversity. This, in turn, modifies the water balance and nutrient cycling of these forests, further complicating the loss of bryophytes and lichens. Shade epiphytes are replaced by sun epiphytes, and species richness diminishes.

In the fragmented Afromontane forests, Malombe *et al.* (2016) found the diversity of epiphyllous bryophytes exhibits no direct correlation with the distance from forest edge. However, they are affected by microenvironmental variables. These variables include tree species composition, sunlight exposure, and canopy structure, all factors that are typically affected by deforestation, even just thinning.

Cloud forests (Figure 45) are unique ecosystems with high bryological diversity and cover in the northern Andes (Benavides & Gutierrez 2011). But this ecosystem is also one of the most endangered ecosystems in the tropics. Agricultural techniques using slash and burn leave behind isolated individual palms in the middle of newly created grasslands or agricultural fields. This isolates the rare canopy bryophyte species. In Colombia, 72 liverwort species and 21 moss species comprised these epiphytic communities. The researchers found a decrease in the number of species from the forest to the grassland. The diversity likewise decreases from base to canopy of palms, with the more common species appearing an average of 4 m lower on the palms in the grassland when compared to those in the forest. The species remaining tend to be drought-tolerant forest species and species that commonly occur in disturbed sites. Hence, these isolated palms do not serve as suitable refugia for the rarer cloud forest species.

Cordova and del Castillo (2001) conducted a chronosequence study exclusively on tree bases in a tropical montane cloud forest in Mexico (Figure 46). The trees examined were in stands of 15, 45, 75, >90 years old, and a primary forest, and had originally been tropical montane cloud forests. They sampled the trees at 1 dm intervals using a sampling grid, up to 160 cm. Total epiphyte cover increases with forest age, following an S-shaped curve. The highest rate of increase is between 15 and 45 years. Whereas moss and liverwort cover increases with stand age, macro- and microlichen cover appear to be independent of age. Cover of microlichens decreases as cover of mosses and tracheophytes increases. Total epiphyte cover per unit area shows some decrease as the diameter of the tree increases.



Figure 45. Cloud forest, Monteverde, Costa Rica. Photo by R. K. Booth, through Creative Commons.



Figure 46. Cloud forest, Bosque Comaltepec, Mexico. Photo by Prsjl, through Creative Commons.

In an assessment of bryophytic epiphytic diversity in Colombian (Figure 47) forest patches, Orrego (2005) suggested that there is a direct relationship between bryophyte species diversity and the structural heterogeneity of forest fragments. He cautioned that a single index is not adequate to assess the epiphytic bryophyte diversity.



Figure 47. Mangrove forest and lowland forest, Ensenada de Utría, Chocó, Colombia. Photo by Philipp Weigell, through Creative Commons.

Gradstein (2008) noted that drought-intolerant species suffer more than drought-tolerant ones under the loss of cover due to deforestation. In the South American tropics, disturbance causes high species turnover and the return to the original epiphytic bryophyte flora is slow. Even after 50 years of forest recovery, the bryophyte flora is still very different from the undisturbed flora. Gradstein and Sporn (2010) documented the tropical diversity of epiphytic bryophytes with land use gradients.

Gradstein and Sporn (2010) summarize the effects of deforestation on the bryophyte communities of the tropics:

1. Deforestation has a significant impact on the bryophyte diversity in what was once forested land. Old secondary forests still experience 0-10% loss, whereas young fallows and cacao agroforest can have 65-80% loss. Epiphytic bryophytes are more strongly affected than are lichens (Gradstein 1992b), with a 4X turnover of bryophytes compared to lichens (Nöske *et al.* 2008). In the arid regions, bryophytes are more sensitive to land use changes than are the tracheophytes (Werner & Gradstein 2009).
2. Life form proportions change in the submontane forests, but not in the montane forests. **Mats** increase in submontane fallows and **tufts** increase in cacao agroforests; this change is accompanied by a loss of **fans**, **pendants**, and **tails**.
3. Shade epiphytes disappear as more exposure is created, and these are replaced by sun epiphytes. Epiphyte heights on the trees experience a shift to lower locations. The canopies become almost devoid of epiphytes.
4. Canopy closure, microclimate, and host tree characteristics serve as drivers of the epiphytic bryophyte diversity under different land-use types, indicating that canopy cover is necessary to maintain the rainforest diversity (Steffan-Dewenter *et al.* 2007). As a result, it may take more than 100 years for the bryophyte diversity to fully recover in second-growth forests.

5. Remnant trees in the pastures can provide a rich habitat where bryophyte species can be conserved. However, some agroforests, such as the cacao agroforest, are unable to provide this role (Andersson & Gradstein 2005).
6. Some bryophyte species can serve as indicators of land-use change at the local and regional scales, but not at larger scales. Qualitative and quantitative study of life forms and ecological groups of epiphytic bryophytes promise to provide bioindication of land-use change and rainforest disturbance in the tropics.

Fragmentation Effects

Deforestation is creating forest fragments in many areas of the tropics (Figure 1). Zartman (2003) discussed the effects of this habitat fragmentation on epiphyllous bryophyte communities in central Amazonia. He found that regionally common taxa are often reduced in epiphyll diversity in small fragments. On the other hand, rare taxa are often more abundant in fragments than in continuous forest habitat. Larger fragments (100 ha) exhibit higher species richness, abundance, and among site variation than do the smaller fragments (1 & 10 ha).

Silva and Pôrto Assessed effects of fragmentation on bryophytes of decaying logs in the Atlantic Forest remnants in northeastern Brazil. They identified 99 bryophyte species (52 liverworts, 47 mosses). They determined that fragment size is important in determining the community structure on decaying logs. They did not find a correlation between distance from forest edge and bryophyte richness or cover, suggesting that the relationship is non-linear.

Zartman and Shaw (2006) consider the demographic mechanisms causing species loss in the tropics to be greatly under-explored. To contribute to the understanding of the impact of fragmentation, they chose the epiphyllous leafy liverworts *Radula flaccida* (Figure 48) and *Cololejeunea surinamensis* (see Figure 49). They transplanted these two species to study sites with areas ranging 1, 10, 100, up to 110,000 ha. All the transplants exhibited significantly positive local growth with a nearly constant per-generation extinction probability of 15%. In reserves of 100 ha or greater, the colonization rate nearly doubled (to 48%) compared to small reserves (27%). They considered this an indication that epiphyll loss in small fragments was due to reduced colonization.



Figure 48. *Radula flaccida* habit with gemmae. Photo by Michaela Sonnleitner, with permission.

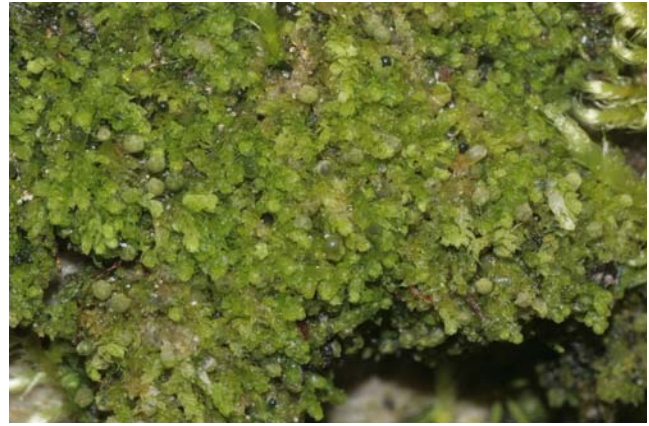


Figure 49. *Cololejeunea calcarea*; *Cololejeunea surinamensis* reproduces more frequently by fragments in larger forest fragments. Photo by Hermann Schachner, through Creative Commons.

Bryophytes have relatively fast colonization and extinction rates, making them ideal study organisms for the effects of forest fragmentation (Pharo & Zartman 2007). Nevertheless, they are limited by dispersal, and this somewhat random process helps to explain their observed recolonization patterns.

Nevertheless, edge effects have an impact on community structure, especially where these create abrupt differences in microclimate. Establishment experiments repeatedly indicate dispersal limitation to explain the absence of typical forest species in fragmented habitats (Zartman & Nascimento 2006; Gunnarsson & Söderström 2007).

Younger fragments (<25 yrs), in particular, have lower richness and different species composition than adjacent mature forests (Pharo *et al.* 2004). Similarly, Snäll *et al.* (2003) found that age of the trees is more important than size for the moss *Orthotrichum* (Figure 50) on aspen (*Populus*; Figure 51) trees. Older trees support larger colonies.



Figure 50. *Orthotrichum* sp. on bark; on aspen trees, age of tree is more important than tree size. Photo by Algirdas, through public domain.



Figure 51. *Populus* bark showing old and young parts of the tree. Photo through public domain.

In southern Veracruz, Mexico, the number of epiphytic tracheophyte species per tree and total estimated biomass correlate most with tree size, measured as diameter at breast height (Hietz-Seifert *et al.* (1996). When considering this relationship, the number of epiphytes on remnant trees is similar to that in the forest plots. However, the forest plots still differ significantly from each other, a response Hietz-Seifert and coworkers considered might be due to differences in humidity. The number of epiphytes on isolated forest tree species exhibit a negative correlation with distance from the forest border. The researchers also considered that some of the differences exhibited by the remnant trees, which included many figs, may have been due to the attraction of birds and bats that could contribute to seed dispersal. Although the importance of various environmental variables differ between bryophytes and tracheophytes, some of these same variables may affect both, and destruction of bryophytic epiphytes can affect the success of tracheophytic epiphytes and *vice versa*.

In open, disturbed areas in the Amazonian Andes of northern Peru, contrasting with the larger life forms of the forests, the disturbed and exposed areas comprising secondary forests are characterized by **short turf-forming** acrocarpous mosses that have a **colonist life strategy**, a life form not typically found within the developed forests (Kürschner & Parolly 1998; Kürschner *et al.* 1999).

Harvesting

Deforestation isn't the only human danger. Harvesting of bryophytes for commercial use likewise can endanger

the bryophytes (Peralta & Wolf 2001). In addition to many Neotropical areas, in India, Japan, and China mats of mosses are peeled from their substrates for use in the horticulture industry (Wuethrich 1993; Peck 2006; Peck & Moyle Studlar 2008). These can greatly reduce cover on the reachable branches and logs.

In the monarch butterfly biosphere reserve, Sierra Chincua, Michoacan, Mexico, mats of bryophytes are harvested, packed, and sold in Mexico City for ornamental use. One family alone (about 10 members) harvested 50 tons (fresh weight) of bryophytes in one collecting season. This created a mosaic of gaps of bare soil in the mossy layer, with an average gap size of 0.48 m². This moss removal consequently caused the removal of 11,000 *Abies* (fir) seedlings that were growing with the mosses.

In the montane tropical oak-bamboo forests in Costa Rica, pendent bryophytes are a locally valuable resource subject to commercial harvesting (Romero 1999). Thus, logging that destroys the habitat of these taxa is of local concern. These harvestable bryophytes include the mosses *Pilotrichella flexilis* (Figure 52-Figure 53), *Phyllogonium viscosum* (Figure 54), *Zelometeorium* sp. (Figure 55), and *Squamidium leucotrichum* (Figure 56) and the leafy liverworts *Frullania convoluta* (Figure 57) and other *Frullania* species. These pendent life forms are important in water interception and thus might be expected to have an important effect on the hydrological balance in these forests. However, nine years after careful selective logging in a montane oak-bamboo forest, there were no detectable negative impacts on the biomass of these bryophytes at commercially available heights (1-3 m). Unfortunately, there is no comparable study in Costa Rica to show the impact of bryophyte harvesting on their successful return. In Africa, Jacobsen (1978) found that epiphytes require a minimum of 7-10 years to regenerate after harvesting from the forest.

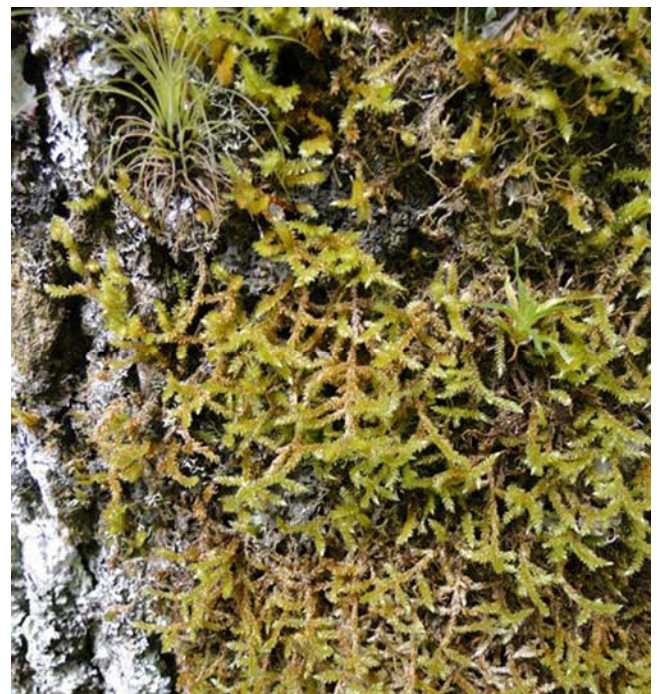


Figure 52. *Pilotrichella flexilis nudiramulosa*, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Claudio Delgadillo Moya, with permission.



Figure 53. Close view of *Pilotrichella flexilis*, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Claudio Delgadillo Moya, with permission.



Figure 54. *Phyllogonium viscosum*, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Jan-Peter Frahm, with permission.



Figure 55. *Zelometeorium patulum* from the Neotropics, a pendent bryophyte in a genus that is used locally in Costa Rica as a forest product. Photo by Michael Lüth, with permission.



Figure 56. *Squamidium leucotrichum* from the Neotropics, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Michael Lüth, with permission.

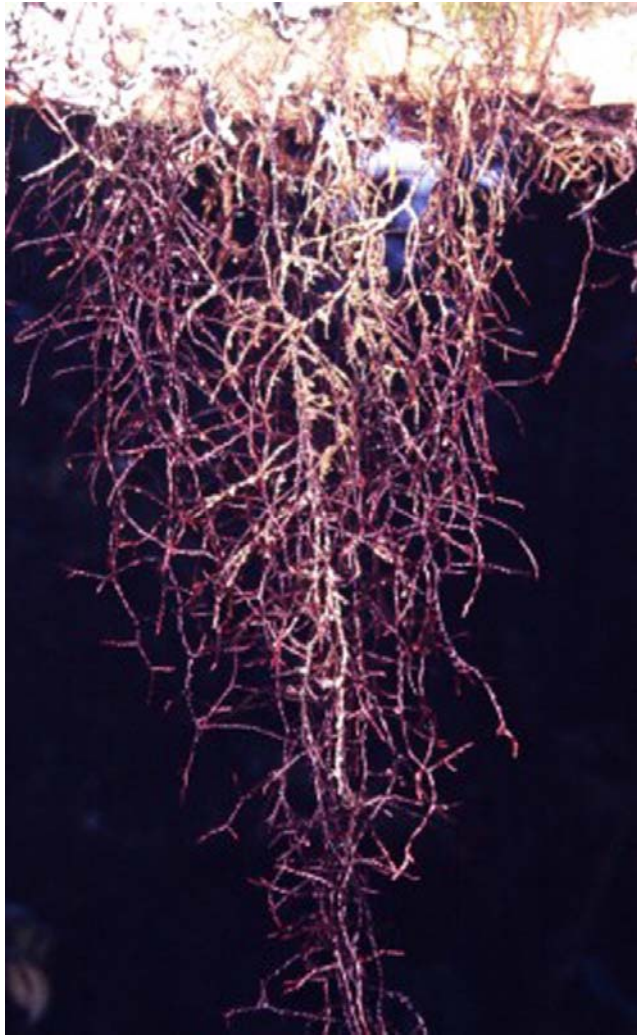


Figure 57. *Frullania convoluta*, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Jan-Peter Frahm, with permission.



Figure 58. *Lejeunea trinitensis*, a stress-tolerant species. Photo by Scott Zona, through Creative Commons.



Figure 59. *Leptolejeunea elliptica*; *L. exocellata* is a stress-intolerant species. Photo by Yang Jia-dong through Creative Commons.

Industrialization and Air Pollution

Escocia Ariza (1998) reported losses of epiphyllous and epiphytic bryophyte species in the 20th century. The industrial district in particular has lower coverage, sexual reproduction, diversity, and a lower index of community vigor. **Chlorosis** (loss of green color of chlorophyll) indicates stress. *Lejeunea trinitensis* (Figure 58) emerged as a stress-tolerant species, whereas *Leptolejeunea exocellata* (Figure 59) is a sensitive species that disappears from the industrialized area. The species present in the polluted area are **colonists**, particularly on rocks. The colonization is a slow process. Species with both sexual and asexual reproduction are more successful at establishment.

Vareschi (1953) was one of the earliest researchers on tropical air pollution in Venezuela. These studies were actually the reverse of most, looking at the influence of the forests and parks on the air quality of the city of Caracas. Rebelo *et al.* (1995) reported on the epiphytic bryophyte communities under the effects of air pollution in Brazil.

In 1992, Durán *et al.* used the Index of Air Purity (IAP) to evaluate the responses of epiphytic mosses to air pollution in Mexico City, Mexico. They were able to demonstrate a significant negative correlation ($p < 0.5$) between these IAP values and SO_2 , NO_2 , NO_x , and Pb (lead). On the other hand, there were significant positive correlations with ozone. This relationship is manifest in the gradual decrease in frequency and cover of epiphytic mosses in Mexico City.

Bryophytes in temperate zones are well known for their ability to accumulate heavy metals (*e.g.* Faus-Kessler *et al.* 2001). But the behaviors of tropical bryophytes are less well known. Based on many temperate studies showing that bryophytes were good accumulators of heavy metals, Lisboa and Borges (1995) examined the potential use of bryophyte diversity as an indicator of pollution in Belém, in the lower Amazon region of Brazil.

Jayasekera and Rossbach (1996) conducted one of the few tropical species to address this issue. They examined background levels of heavy metals and their differences in plants of different taxonomic groups, including bryophytes, in a montane rainforest in Sri Lanka. They found that when a lichen (*Usnea barbata*; Figure 60/61), an epiphytic club moss (*Huperzia selago*; Figure 62), an epiphytic fern (*Pleopeltis lanceolata*; Figure 63), an epiphytic orchid (*Bulbophyllum elliae* (see Figure 64), a large dicotyledonous tree (*Actinodaphne ambigua*; see Figure 65) and a moss [*Pogonatum* sp. (Figure 66)] were compared for their heavy metal content, the levels were essentially homogeneous for Cd, Cu, Pb, and Zn. The moss *Pogonatum* had the highest degree of homogeneity for lead. The primitive taxa, the lichen *Usnea* and moss *Pogonatum* seem to have higher accumulation levels of As, Cd, Co, and Pb than do the tracheophytes.



Figure 60. *Usnea* from Cumbre Vieja, Canary Islands, a genus used locally in Costa Rica as a forest product. Photo by Fährtenleser, through Creative Commons.



Figure 61. *Usnea barbata*, a fruticose lichen with higher accumulations of Cd, Cu, Pb, and Zn levels than surrounding tracheophytes. Photo from MO Observers, through Creative Commons.



Figure 62. *Huperzia selago*, a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Malcolm Storey, DiscoverLife, with online permission.



Figure 63. *Pleopeltis lanceolata*, a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Robbin Moran, with permission.



Figure 64. *Bulbophyllum guadense*; *Bulbophyllum elliae* is a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by USDA & GPEPP, through Creative Commons.



Figure 65. *Actinodaphne angustifolia*; *Actinodaphne ambigua* is a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Dinesh Balke, through Creative Commons.



Figure 66. *Pogonatum urnigerum*, a species that has a high degree of homogeneity for absorbing lead. Photo by David Holyoak, with permission.

Faus-Kessler *et al.* (2001) used biannual collections of epiphytic *Hypnum cupressiforme* (Figure 67) to determine changes in accumulations of trace metals.



Figure 67. *Hypnum cupressiforme*, a species used for determining accumulations of trace metals. Photo by Aconcagua, through Creative Commons.

On the other hand, bryophytes have been used to help clean the air and remove pollutants (Vareschi 1953). Bryophytes greatly expand the available surface area for trapping and immobilizing both water and ions from the atmosphere (Coxson 1991).

Radiation

Although the studies on radiation effects on tropical bryophytes are limited, the extensive study at El Verde, Puerto Rico (Figure 68), did include bryophytes (Odum *et al.* 1970). High levels of radiation fallout retention were present in the epiphytic mosses in the mossy forest (Figure 69) of the Luquillo Mountains in 1962. The algae-moss-liverwort encrustations had the highest levels of radiation, with massive moss colonies being second. Bromeliads and rooted plants had less. Radioactivity in tree leaves was in proportion to the epiphyllous growths on them, and that growth was related to leaf age.



Figure 68. Rainforest of El Yunque, Puerto Rico, where the El Verde radiation study site is located. Photo by Alessandro Cai, through public domain.



Figure 69. Elfin forest at the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.

Man-made Habitats

Many forested areas have been replaced by man-made habitats. These provide greater variety in available habitats. In the tropics, one can find *Diplophyllum obtusatum* (Figure 70), *Solenostoma sphaerocarpum* (Figure 71), and *Schistochilopsis incisa* (Figure 72) in man-made habitats (Gradstein & Vána 1987). It appears that these Laurasian species have spread relatively recently through human activities.



Figure 70. *Diplophyllum obtusatum*, a species that thrives in man-made habitats. Photo by Paul Davison, with permission.



Figure 71. *Solenostoma sphaerocarpum*, a species that thrives in man-made habitats. Photo by Michael Lüth, with permission.



Figure 72. *Schistochilopsis incisa*, a species that thrives in man-made habitats. Photo by Michael Lüth, with permission.

In Alto Beni, Bolivia, corticolous bryophytes on trees in the primary rainforest decreased significantly in the fallows as measured after 4-15 years (Cabby *et al.* 2003). But liverwort diversity barely changed except in the 4-year-old forest. Smooth mats had a significantly higher percentage (72%) in the fallows, perhaps due to the warmer, drier microclimate. But even in the 10-15-year-old fallows, only about half the species had returned, mostly generalists and sun epiphytes. Whereas species richness is highest in the undisturbed canopy, in the fallows it is highest in the understorey, with rough mats, fans, and tails shifting to lower heights on the trees, most likely due to changes in air temperature and air humidity.

If sufficient natural forest is retained, artificial forests can increase the diversity by providing new niches. Petit and Symons (1974) reported 28 bryophyte species from 17 artificial woodlands planted with *Cupressus* (Figure 73-Figure 74) and *Acacia* (Figure 22) in Burundi, Africa. In these woods, the litter layer is covered with bryophytes and the flowering plants are almost absent.



Figure 73. *Cupressus lusitanica* (= *Hesperocyparis lusitanica*) cones; this species is the most commonly harvested *Cupressus* species in Burundi. Photo from Wikimedia, through Creative Commons.



Figure 74. *Cupressus lusitanica* (= *Hesperocyparis lusitanica*) being harvested in Uganda. Photo by J. D. Ward, USDA Forest Service, <Bugwood.org>, through Creative Commons.

Sillett *et al.* (1995) compared bryophyte diversity in *Ficus* tree crowns from the cloud forest and a pasture in Costa Rica. In the lower montane wet forest, they found 127 bryophyte species (50 mosses, 76 liverworts, 1 hornwort) in the inner crowns of only six *Ficus tuerckheimii* trees. Of these, 52 were found only in the intact forest, whereas only 18 species occurred exclusively in the isolated trees of the pasture. One of the factors contributing to the differences was a moisture gradient that diminished away from the intact forest.

In the northern Andes, roadside habitats in humid locations can be invaded by canopy liverworts from the montane forest (Gradstein 1992b). These include such liverwort species as *Dicranolejeunea axillaris*, *Frullania brasiliensis* (Figure 75), *Frullania convoluta* (Figure 57), *Frullanoides densifolia* (Figure 76), *Herbertus acanthelius* (see Figure 77), *Jamesoniella rubricaulis* (Figure 78), *Omphalanthus filiformis* (Figure 79), and *Taxilejeunea pterigonia* (see Figure 80). In such locations these liverworts behave as pioneers.



Figure 75. *Frullania brasiliensis*, a species that inhabits wet roadside habitats in the northern Andes. Photo by Germaine A. Parada, through Creative Commons.



Figure 76. *Frullanoides densifolia*, a species that inhabits wet roadside habitats in the northern Andes. Photo by Jan-Peter Frahm, with permission.



Figure 77. *Herbertus* sp., Oahu, Hawaii; *Herbertus acanthelius* inhabits wet roadside habitats in the northern Andes. Photo by David Eickhoff, with online permission.



Figure 78. *Jamesoniella rubricaulis*, a species that inhabits wet roadside habitats in the northern Andes. Photo by Jan-Peter Frahm, with permission.



Figure 79. *Omphalanthus filiformis*, a species that inhabits wet roadside habitats in the northern Andes. Photo by Michael Lüth, with permission.



Figure 80. *Taxilejeunea* sp. from the Neotropics; *Taxilejeunea pterigonia* inhabits wet roadside habitats in the northern Andes. Photo by Michael Lüth, with permission.

Climate Change

Benzing, in 1998, stressed the vulnerabilities of tropical forests to climate change, and even more so to that of their bryophytic inhabitants. Noting the complexity of these systems, he pointed to the narrow set of circumstances that define the habitats for these bryophytes. This raises the concern of their often underestimated role in both hydrology and mineral cycling, added to their ability to support a wide diversity of smaller organisms such as salamanders, arthropods, fungi, and micro-organisms, makes them major contributors to the ecosystem. Yet their vulnerability in tropical forests under climate change is great.

Many bryophytes in the tropics are approaching their limits of tolerance to the high temperatures that increase their rate of respiration (see Microclimate above). Hence, as considered by Zotz and Bader (2009), "rising temperatures could have disastrous effects." Moving farther away from the equator may provide a refuge for some species, but the authors suggest that epiphytes may be "particularly threatened" because the cloud forest habitats are likely to be the most seriously affected. And these are

species-rich habitats where "exceptional" species occur. They furthermore are often isolated, requiring long-distance dispersal to reach a suitable climate.

Durán *et al.* (1992) used the IAP values to demonstrate that higher rainfall and relative humidity helped to account for higher bryophyte diversity values. Climate changes can affect these parameters, making some areas drier. Furthermore, bryophyte IAP values exhibit a negative correlation with temperature.

Climate change studies in the tropics are of utmost importance in a region where many species are already limited by temperature. Jácome *et al.* (2011) summarized what we know about the effects on the epiphytic bryophyte communities of simulated climate change in the tropics. Based on a translocation experiment in the upper montane forest in Bolivia they showed that exposure to air temperature increases of 1.5-2.5°C had a measurable effect on the structure of epiphytic bryophyte communities of the tropical montane forest within two years. The results confirm the sensitivity of non-tracheophytic epiphytes to atmospheric changes and predict that changes in the climatic regimes of tropical montane forests will rapidly affect the rich non-tracheophytic epiphyte communities.

Epiphytes seem to be particularly vulnerable to climate change because they must survive "at the interface of vegetation and atmosphere" (Zotz & Bader 2009). Furthermore, land use exacerbates the problem by decreasing the suitability of the environment. On the other hand, some drought-resistant species may benefit. They projected that new assemblages would form among bryophytes and lichens. But rising temperatures can be very destructive for both bryophytes and lichens. This will most likely be most detrimental to the habitats in the tropics with exceptional species richness, in particular, the cloud forests.

Sometimes human interference resulting in local climate change actually helps bryophytes. Kautz and Gradstein (2001) found that the critically endangered *Spruethanthus theobromae* (Lejeuneaceae; Figure 19) grows on the trunk bases of *Theobroma cacao* (Figure 20-Figure 21) in 12 plantations that had minimal management. In fact, the researchers felt that it should instead be considered as a near-threatened species and removed from the World Red List.

Recovery

Hallingbäck and Tan (1996) bemoaned the loss of species worldwide, citing reduction, fragmentation, and isolation of their habitats, in addition to damaging pollution. They noted the value of designating certain bryophytes as key species to protect because of the associated plants and animals that would also be protected. But if areas already impacted are allowed to recover, what can we expect?

Gradstein and Sporn (2010) found that canopy closure, microclimate, and host tree characteristics are important in determining epiphytic bryophyte diversity. Preservation of the canopy, therefore, is important in maintaining this diversity. Recovery of bryophyte communities after clear-cutting is very slow and may take more than 100 years.

Recovery following deforestation requires the presence of viable plant parts or reproductive units. Olarinmoye (1986), working in Nigeria, examined survival strategies in

three species during re-establishment after a period of drought. *Hyophila involuta* (Figure 81-Figure 82) is able to re-establish through spores, with its sporophyte production appearing to give it a competitive advantage compared to *Barbula indica* (Figure 83) and *Fissidens asplenoides* (Figure 84). The latter two species were similarly wide-spread, using vegetative regrowth from rhizoids, shoot bases, apices, or the main stem, with rhizoids contributing the most regrowth.



Figure 81. *Hyophila involuta*, a species that can recolonize disturbed areas. Photo by Shyamal L., through Creative Commons.



Figure 82. *Hyophila involuta*, a species that can colonize by spores after disturbance. Photo by M. C. Nair, K. P. Rajesh, and Madhusoodanan, through Creative Commons.



Figure 83. *Barbula indica*, a species that can colonize deforested areas by vegetative means. Photo by Michael Lüth, with permission.



Figure 84. *Fissidens asplenoides*, a species that can colonize deforested areas by vegetative means. Photo by David Tng, with permission.

Liu *et al.* (2007) elaborated the species on the forest floor and on the tree trunks in the forest of Heishiding Nature Reserve, Guandong, China. They found that species composition of the mature forest was similar to that of the mixed pine and broad-leaved forest, and to young secondary forest, but community structure of the mature forest was quite different from that of the secondary forest. Most of the bryophytes occurred on the tree trunks (40 species), with only 24 species on the forest floor. Bryophyte cover was low on both substrata. Species richness of forest floor bryophytes in 2,500 m² quadrats ranged 8 to 13 with 0.59% to 1.12% cover. Slope and microenvironment were the primary determinants of species distribution and richness on the forest floor. Epiphytes, on the other hand, exhibited 12 to 20 species with a mean cover of 0.63 to 1.63% in these plots. The researchers concluded that bryophytes in 30-year-old secondary broad-leaved forest had returned to the level of the mature broad-leaved forest.

Corrales *et al.* (2010) recorded 151 terrestrial bryophyte species in secondary and planted montane forests in the northern portion of the Central Cordillera of Colombia. Secondary montane forests have a higher weighted species richness than do the pine plantations. Weighted species richness is higher in secondary montane forests and cypress plantations than in pine plantations. Cypress plantations have the highest bryophyte abundances, although Detrended Correspondence Analysis indicates a high floristic similarity among the various forest types. Differences seem to relate to soil pH, slope, and light availability. Regional patterns depend on continuous dispersal of propagules.

Serrano (1996) found 37 species of mosses in 25 genera in disturbed areas in the municipality of Bayamon, Puerto Rico. *Fissidens* is the most species-rich genus. The most frequent of all species is *Fissidens zollingeri* (see

Figure 84), occurring at all study sites. It is an indicator of disturbed areas. Urbanization further reduces the number of species present. One mechanism accounting for the spread of the species is spore production. Of the 37 species, 18 were observed with capsules and these species tended to occur more frequently when their sporophytes were more frequent. Only 7 species exhibited special vegetative reproductive structures. Among the pleurocarpous species, those with the greatest frequency in collections were those colonizing the greatest number of substrates.

Conservation Issues

Gradstein (1992a, b) and Pócs (1996) emphasized that conservation of epiphytes "can only be achieved through the rigorous protection of the forests."

Plantations seem to have positive and negative effects on bryophyte diversity. One problem they create is a reduction in the number of niches (Ramovs & Roberts 2005; Yan *et al.* 2013). Their reduction in substrates includes absence of rotten logs and tip-up mounds, substrates that typically have at least some differences in species from typical epiphytic habitats.

Deforestation (Figure 85) has greatly reduced diversity of bryophytes, as one might expect. The loss of the high canopy has forced species that typically occupy the canopy to appear as low as the base of the tree (Gradstein 2002). This change in position correlates with the microclimate of the canopy in the mature forest, with the microclimate in the fallows matching closely the humidity and air temperature of the mature canopy. Such is not the case with the microclimate of the tree bases under the mature canopy.



Figure 85. Deforestation in the Amazon forest. Photo by Matt Zimmerman, through Creative Commons.

Henderson *et al.* (1991) reported that approximately 90% of the South American tropical mountain forests had been converted into pastureland or other non-forest use. Bryophyte losses are greater among mosses than among liverworts (Jácome *et al.* 2011). Shade species are more affected than drought-tolerant canopy species. The latter species are able to grow in lower positions on the remaining trees. A dense canopy is important in maintaining high diversity (Steffan-Dewenter *et al.* 2007;

Sporn *et al.* 2009). Despite the negative impact, in Costa Rica the secondary forests may have up to 40% of their epiphytic species exclusively in the secondary forest.

When the cacao (Figure 20-Figure 21) culture was expanded by 230% by converting tropical rainforests, there was little effect on the overall species richness, but plant biomass and carbon storage were reduced by approximately 75% (Steffan-Dewenter *et al.* 2007). Species richness of forest species was reduced by approximately 60%. More intense agriculture and reduced shade by agroindustry of cacao plantations reduced shade cover from 80% to 40%, but only minor quantitative changes occurred in biodiversity. Unfortunately for the forests and their bryophytes, unshaded systems increased income by 40%. Intermediate levels of canopy cover seemed best for species richness of herbs, bees, wasps, and their antagonists. On the other hand, bryophytes, canopy beetles, and ants lack any significant correlation with canopy cover. This may be because only a small fraction of the forest herb, bryophyte, and beetle species were also able to colonize the agroforestry systems.

When epiphytes were transplanted to lower elevations in the Bolivian Andes, the cover became more even and dominance of individual species decreased (Jácome *et al.* 2011). The researchers concluded that as the climate changes the individual species responses will differ, resulting in new community relationships. They warn that short-term responses might not be indicative of long-term responses.

Pócs (1989) reported that epiphytes are much rarer in disturbed forests than they are in undisturbed forests in submontane rainforests in the East Usambara Mountains of East Africa. Rather, the species in the disturbed forests are sun species and occur on the lower parts of trunks of *Maesopsis* (umbrella tree; Figure 86). In the undisturbed forests, these same species occur in the canopy. Pócs has also found a decline in epiphytes in the "undisturbed forest." He attributed this to the drying climate.

Hallingbäck and Hodgetts (2000) contend that the negative impact of habitat loss has already gone too far in the tropical lowlands. Forested land has been cleared continuously for the expansion of the human population and the agriculture to support it (Hyvönen *et al.* 1987).

Costa and Faria (2008) noted conservation priorities for bryophytes in the state of Rio de Janeiro, Brazil. Recognizing the high degree of biological diversity, with an estimated 1,040 species of bryophytes, they cautioned that most of the inventories have focussed on the montane rainforest and coastal region. Among those bryophytes that have been recorded, 14% are considered vulnerable or threatened in the region. They considered the old-growth Atlantic forests to be among most important habitats needing conservation, citing reduction, fragmentation, and isolation as causes for concern. Although 13% of the land area of the state is protected, these protected areas are mostly montane and upper montane Atlantic rainforests.

Alvarenga *et al.* (2009b) likewise reported a highly significant loss of richness as a result of habitat loss in a Brazilian Atlantic forest. The most conserved fragments have more than 10 times the species richness of the least conserved fragment. In non-conserved fragments, the epiphytes do not colonize the lower trunks (2.1-10 m) or higher zones. Instead, they are restricted to the lowest 2 m

at the tree base and clearly exhibit an altered floristic composition. Specialists of sun or shade are impacted more than generalists. The generalists decrease in richness in non-conserved habitats, but their proportion increases due to the loss of specialists. The habitats that retain their rich epiphyte flora are greater than 300 ha in size – an uncommonly large size in the Brazilian Atlantic rainforest.



Figure 86. *Maesopsis eminii* (umbrella tree) providing shade for a coffee plantation. Photo by Aniruddha Dhamorikar, through Creative Commons.

Holz and Gradstein (2005) found that total species richness of bryophytes and lichens differs little between primary and early or late secondary upper montane *Quercus copeyensis* forests (Figure 87) of Costa Rica. The high richness in the secondary forest is most likely due to the high humidity under the closed canopy. Nevertheless, species composition differs markedly. After 40 years of recovery, 46 (one-third) of the species still had not become re-established. Of all recorded species, 40% (68 species) occur exclusively in the secondary forests.

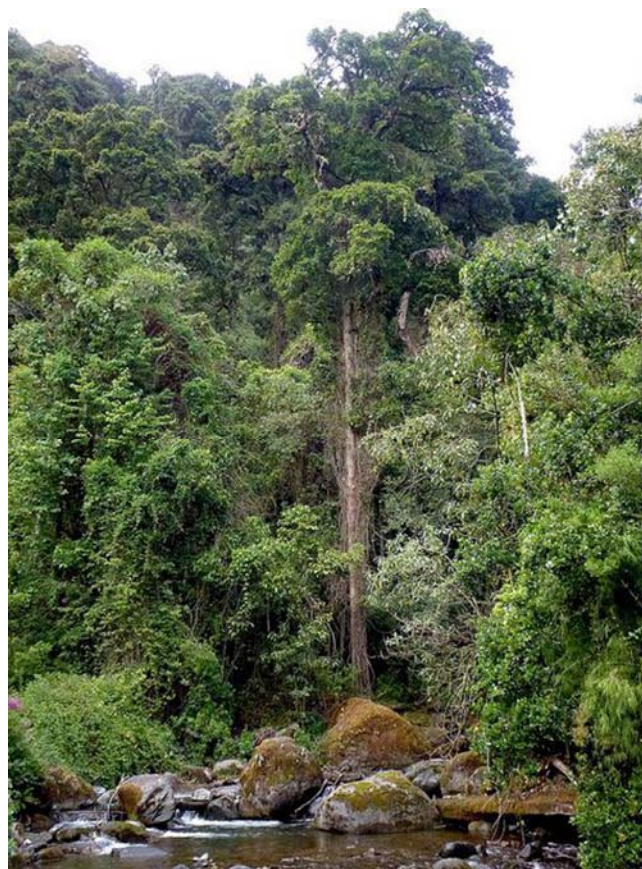


Figure 87. *Quercus copeyensis* forest wherein species richness differs little between primary and secondary forest, but the kinds of species differ. Photo through Creative Commons.

In addition to habitat loss, pollutants can destroy canopy bryophytes. Bryophytes are scavengers of atmospheric nitrogen as they collect the dust from the atmosphere. In this way, they are able to serve as bio-indicators of nitrogen pollution. Shi *et al.* (2017) examined epiphytic bryophytes from a subtropical montane cloud forest in southwest China. The critical load of nitrogen deposition there was estimated at $18 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The bryophytes become nutrient pools in these circumstances. These high levels are detrimental to the bryophytes, with a significant decrease in cover when the nitrogen input is only $7.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The study site had a nitrogen deposition rate of $10.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The researchers suggested that the high N levels not only did direct damage, but caused the leakage of magnesium and potassium, both essential nutrients for cellular metabolism.

Plantations seem to have both positive and negative effects on bryophyte diversity. One problem they create is a reduction in the number of niches (Roberts *et al.* 2005). Their reduction in substrates includes absence of rotten logs and tip-up mounds, substrates that typically have at least some differences in species from typical epiphytic habitats.

Deforestation (Figure 1, Figure 85) has greatly reduced diversity of bryophytes, as one might expect. The loss of high canopy has forced species that typically occupy the canopy to appear as low as the base of the tree (Gradstein 2002). This change in position correlates with the microclimate of the canopy in the mature forest, with the microclimate in the fallows matching closely the humidity

and air temperature of the mature canopy. Such is not the case with the microclimate of the tree bases under the mature canopy.

When epiphytes were transplanted to lower elevations in the Bolivian Andes, the cover became more even and dominance of individual species decreased (Jácome *et al.* 2011). The researchers concluded that as the climate changes the individual species responses will differ, resulting in new community relationships. They warn that short-term responses might not be indicative of long-term responses.

Pócs (1989) reported that epiphytes are much rarer in disturbed forests than they are in undisturbed forests in submontane rainforests in the East Usambara Mountains of East Africa. Rather, the species in the disturbed forests are sun species and occur on the lower parts of trunks of *Maesopsis* (Figure 86). In the undisturbed forests, these same species occur in the canopy. Pócs has also found a decline in epiphytes in the "undisturbed forest." He attributed this to the drying climate.

Climate change studies in the tropics are of utmost importance in a region where many species are already limited by temperature. Jácome *et al.* (2011) summarized what we know about the effects on the epiphytic bryophyte communities to simulated climate change in the tropics.

Jacobsen (1978) found that epiphytes require a minimum of 7-10 years to regenerate after harvesting of the forest. In any case, deforestation leads to local extinction of species (Gradstein 1992b). Shade epiphytes are the most easily affected by disturbance.

Hallingbäck and Hodgetts (2000) contend that the negative impact of habitat loss has already gone too far in the tropical lowlands. Forested land has been cleared continuously for the expansion of the human population and the agriculture to support it (Hyvönen *et al.* 1987). In India, Japan, and China mats of mosses are peeled from their substrates for use in the horticulture industry (Peck 2006).

Alvarenga *et al.* (2009b) likewise reported a highly significant loss of richness as a result of habitat loss in a Brazilian Atlantic forest (Figure 88). The most conserved fragments had more than 10 times the species richness of the least conserved fragment. In non-conserved fragments, the epiphytes did not colonize the lower trunks (2.1-10 m) or higher zones. Instead, they were restricted to the lowest 2 m at the tree base and clearly exhibited an altered floristic composition. Specialists of sun or shade were impacted more than generalists. The generalists decreased in richness in non-conserved habitats, but their proportion increased due to the loss of specialists. The habitats that retained their rich epiphyte flora were greater than 300 ha in size – an uncommonly large size in the Brazilian Atlantic rainforest.

In addition to habitat loss, as seen above, pollutants can destroy canopy bryophytes. Bryophytes are scavengers of atmospheric nitrogen as they collect the dust from the atmosphere. In this way, they are able to serve as bio-indicators of nitrogen pollution. Shi *et al.* (2017) examined epiphytic bryophytes from a subtropical montane cloud

forest in southwest China. The critical load of nitrogen deposition there is estimated at $18 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The bryophytes become nutrient pools in these circumstances. These high levels are detrimental to the bryophytes, with a significant decrease in cover when the nitrogen level is only $7.4 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The study site had a nitrogen deposition rate of $10.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The researchers suggest that the high N levels not only do direct damage, but cause the leakage of magnesium and potassium, both essential nutrients for cellular metabolism.



Figure 88. Atlantic Forest, Antonina Bay, Brazil. Photo by Deyvid Setti and Eloy Olindo Setti, through Creative Commons.

The International Association of Bryologists has representation on the IUCN (International Union for Conservation of Nature). To quote Söderström *et al.* (1992), "The conservation process involves recognizing and listing rare and decreasing species, recording their distribution, biology and specific threats, proposing conservation programmes, and executing these programmes." But they point out that the large gaps remaining in our knowledge about bryophytes complicate conservation practices. They list areas needing further study, including taxonomy, bryogeography, habitat demands, natural dynamics, dispersal ability, population structure, and genetics. They stress the importance of focussing on conservation of habitats and sites where species can survive on their own.

In this regard, Villaseñor *et al.* (2006) gathered data on the rich moss and *Senecio* (Figure 89) flora in the Trans-Mexican volcanic belt. They were able to identify 11 hotspots that are beneficial to the rich species composition of both groups. They conclude that 18 "cells" in this range would conserve the total diversity of both mosses and *Senecio* species in these species-rich hotspots.



Figure 89. *Senecio tolucanus*, a common species of the Trans-Mexican volcanic belt. Photo by Juan Carlos Pérez Magaña, through Creative Commons.

Twenty years ago, our knowledge of tropical bryology was quite meager, making conservation efforts problematic. Sastre de Jesus and Tan (1995) noted the problems in Puerto Rico and the Philippines. As noted by Streimann (1994) for Australia, conservation programs must be preceded by a good knowledge of the bryophytes. In absence of those data, he recommended that at least for those areas that are poorly known for bryophytes, those areas conserved for vascular plants, including national parks and forest reserves, would in most cases be adequate to conserve bryophytes as well.

The bryophyte flora of Mexico was somewhat better known, with more than 900 species, including 98 endemic taxa (Delgadillo 1996). Even so, many areas still need to be explored. Meanwhile, habitat destruction may be destroying some taxa forever. Delgadillo bemoaned the fact that there still was no legislation to protect the habitats of any Mexican mosses.

As in Mexico, moss diversity in the tropical Andes is extensive, with 2,058 species known in 1995. Although this number is probably inflated due to the same species being named multiple times in different locations, the presence of 343 genera and 75 families is still an indicator of the high diversity. Churchill *et al.* (1995a) estimate the actual number to be 1,500-1,700. They contend that the tropical Andes are eight times as rich in moss species as the Amazon basin. Churchill (1996) summarized the status of

our knowledge of moss diversity and conservation in the Andes, noting the needs to prepare for the future.

One of the problems with conserving bryophytes in Neotropical cloud forests (Figure 45) is that they are typically surrounded by xeric habitats unsuitable for their survival (Churchill *et al.* 1995b).

The Neotropics are not the only tropical area experiencing serious species loss. Turner *et al.* (1994) reported extinction of 594 of the 2,277 tracheophyte species in the Republic of Singapore. Epiphytic species have suffered 62% loss. These losses are due to deforestation (99.8% of primary forest) and disturbance, with the mangrove epiphytic flora disappearing completely. These losses will necessarily impact the losses of bryophytes through loss of substrate, shade, and sufficient humidity.

Holz and Gradstein (2005) considered that genera and species of bryophytes and macrolichens that are exclusive to the primary (uncut) forests could be used as indicator taxa and that these species and their forests should be conserved.

In French Guiana, water availability affects the bryophyte life forms. When Pardow *et al.* (2012) compared the life forms of the lowland cloud forests with those of the other lowland forests, they concluded that life forms could indicate lowland cloud forests that are appropriate for conservation. This would permit conservation of a rich bryophyte flora with higher biomass and cover.

With 1,000 epiphyllous liverworts worldwide, these tiny plants represent a group that is also endangered worldwide (Pócs 1996). Of these, 504 are in Asia and 375 in the Americas. They are by far the most species rich in the tropical and subtropical rainforests, but as these forests disappear, so do the epiphylls.

Newer tools may help us to process the data in meaningful ways to understand environmental impacts. In summarizing the symposium and priorities for future research, presented at the first IAB and IAL Symposium on Follicolous Cryptogams, Gradstein and Lücking (1997) noted that multivariate statistical methods were useful in analyzing the follicolous community data.

With the inevitability of global climate change, bryophytes living in tropical mountain habitats are clearly in danger. Zhang (2001) found a linear increase in number of species per forest plot with an increase in altitude. As those areas become warmer, those species may not have the time needed for significant dispersal to distant areas with a similar cool climate.

Gradstein and Pócs (1992a) advised that protection of as much as possible of the remaining natural tropical rainforest area seems the best approach to the conservation of the tropical bryophyte flora.

Current Status

In 1982, Schultze-Motel referred to the crisis in tropical bryology. Part of this crisis is the loss of habitats and species before we have even explored to determine what is there to be lost. Even worse, we know little of their role in these sensitive, disappearing ecosystems, even today.

In 1992, Motito *et al.* recognized the need for bryological study in Cuba (Figure 90). At that time 383

infrageneric bryophyte taxa were known, and studies had begun on phytochemistry and antibiosis. However, it seems that little progress has been made since then on protection of species or of understanding their ecology.



Figure 90. Montane moist forest, Pico Turquino, Cuba. Photo by Male Gringo, through Creative Commons.

In Brazil, biological diversity is high, particularly in the state of Rio de Janeiro (Figure 91). In this area, there are many bryophyte endemics with a total species number estimated at ~1,040 species. Of these, 150 species are classified as vulnerable or threatened. Unfortunately, many of the 1,040 species are in the "data deficient" category, so their abundance is not known, nor do we know what conditions are needed to maintain them. Fortunately, almost 13% of Rio de Janeiro is protected land, but it is mostly in the montane and upper montane Atlantic rainforests. The remaining old-growth Atlantic rainforests are in need of greater conservation.



Figure 91. Rio de Janeiro Tijuca Forest, Brazil. Photo by Pierre André, through Creative Commons.

Summary

Natural disturbances such as El Niño, hurricanes, fire, volcanoes, and animal activity can dislodge bryophytes or provide conditions unsuitable to their continued growth. Some rare and threatened species

thrive in these altered conditions, but in general these are potential sources of species losses.

Disturbance is a major cause of loss of species and populations in the tropics. Approximately half of the bryophyte taxa lost on fallow land can become re-established in 10-15 years; most of these are ecological generalists and sun-loving epiphytes. For others it can take 100 years. Sufficient fragment size is important in maintenance and re-establishment of species.

The highest diversity of the fallows is in the understory, contrasting with the highest richness in the canopy of the uncut rainforest. This difference is the result of light penetration, and in some cases moisture.

Human harvesting of bryophytes for horticulture and other human uses not only reduces the bryophyte cover, but also removes habitat for numerous invertebrates and many amphibians.

Industrialization can raise nitrogen levels beyond the limits of tolerance. Heavy metals accumulate in the bryophytes and can reach lethal levels. On the other hand, the bryophytes can serve as filters to remove these pollutants from the air, in some cases after the bryophytes die.

Man-made habitats displace natural habitats, but they do increase the number of niches. Some species thrive in these new niches. For example, the leafy liverwort *Sprutheanthus theobromae* is currently known from the bark of cacao on plantations.

Many bryophytes have narrow temperature, light, and moisture requirements. Changing climate can not only destroy the forests where they live, but change the microclimate so that it is no longer suitable for them.

Bryophyte recovery can take a long time. In particular, those species living on mountain tops may not have any suitable propagule source without intervening unsuitable habitats. Even in restored lowland rainforests, recovery of bryophyte diversity can require more than 100 years.

The most pressing issues seem to be massive losses of habitat due to agriculture and forestry management for trees only. But climate change is likely to be a close second in the loss of tropical bryophytes in the tropics.

Current practices are beginning to recognize that some species can be conserved by maintaining larger fragments, keeping more trees where trees are cut, and designating more land to conservation.

Acknowledgments

My appreciation goes to Robbert Gradstein for his efforts to make this subchapter complete and up-to-date. His many publications, his contribution of images, his mentoring of students, and his helpful comments on a very early version of the chapter kept me going on this part of the world I know so little about.

Literature Cited

Acebey, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in

- submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.
- Achard, F., Eva, H. D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T., and Malingreau, J.-P. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* 297: 999-1002.
- Ah-Peng, C., Chuah-Petiot, M., Descamps-Julien, B., Bardat, J., Stamenoff, P., and Strasberg, D. 2007. Bryophyte diversity and distribution along an altitudinal gradient on a lava flow in La Réunion. *Divers. Distrib.* 13: 654-662.
- Alvarenga, L. D. P., Pôrto, K. C., and Silva, M. P. 2009. Relations between regional-local habitat loss and metapopulation properties of epiphyllous bryophytes in the Brazilian Atlantic Forest. *Biotropica* 41: 682-691.
- Andersson, M. S. and Gradstein, S. R. 2005. Impact of management intensity on non-vascular epiphyte diversity in cacao plantations in western Ecuador. *Biodiv. Conserv.* 14: 1101-1120.
- Ariyanti, N. S., Bos, M. M., Kartawinata, K., Tjitrosoedirdjo, S. S., Guhardja, E., and Gradstein, S. R. 2008. Bryophytes on tree trunks in natural forests, selectively logged forests and cacao agroforests in Central Sulawesi, Indonesia. *Biol. Conserv.* 141: 2516-2527.
- Batke, S. P. and Kelly, D. L. 2015. Changes in the distribution of mechanically dependent plants along a gradient of past hurricane impact. *AoB Plants* 7. Available at <<https://academic.oup.com/aobpla/article/doi/10.1093/aobpla/plv096/1800685>>.
- Baudoin, R. 1985. Analyse de la distribution des bryophytes épiphyllous sur la soufrière de Guadeloupe. *C. R. Séances Soc. Biogéogr.* 61: 47-57.
- Benavides, J. C. and Gutierrez, C. A. 2011. Effect of deforestation in palm-epiphytic bryophyte communities in a cloud forest in the northern Andes. *Bryologist* 114: 155-165.
- Benítez, Á., Prieto, M., and Aragón, G. 2015. Large trees and dense canopies: Key factors for maintaining high epiphytic diversity on trunk bases (bryophytes and lichens) in tropical montane forests. *Forestry* 88: 521-527.
- Benzing, D. H. 1998. Vulnerabilities of tropical forests to climate change: The significance of resident epiphytes. *Climatic Change* 39: 519-540.
- Bruijnzeel, L. A. and Proctor, J. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? In: Hamilton, L. S., Juvik, J. O., and Scatena, F. N. (eds.). *Tropical Montane Cloud Forests*, Ecological Studies vol. 110, Springer-Verlag, New York, N. Y., pp. 38-78.
- Cabby, A., Gradstein, S. R., and Krömer, T. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. *J. Trop. Ecol.* 19: 9-18.
- Chapman, W. S. and King, G. C. 1983. Floristic composition and structure of a rainforest area 25 years after logging. *Austral. J. Ecol.* 8: 415-423.
- Churchill, S. P. 1996. Andean moss diversity and conservation: State of knowledge and prerequisites for the future. *An. Inst. Biol. Univ. Nac. Auton. Mexico* 67: 169-176.
- Churchill, S. P., Griffin, D. III, and Lewis, M. 1995a. Moss diversity of the tropical Andes. In: Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, N. Y.
- Churchill, S. P., Balslev, H., Forero, E., and Luteyn, J. L. (eds.). 1995b. *Biodiversity and Conservation of Neotropical Montane Forests*. New York Botanical Garden, N. Y.
- Cordova, J. and Castillo, R. F. del. 2001. Changes in epiphyte cover in three chronosequences in a tropical montane cloud forest in Mexico. Life forms and dynamics in tropical forests. *Diss. Bot.* 346: 79-94.
- Corrales, A., Duque, A., Uribe, J., and Londoño, V. 2010. Abundance and diversity patterns of terrestrial bryophyte species in secondary and planted montane forests in the northern portion of the Central Cordillera of Colombia. *Bryologist* 113: 8-21.
- Costa, D. P. 1999. Epiphytic bryophyte diversity in primary and secondary lowland rainforests in Southeastern Brazil. *Bryologist* 102: 320-326.
- Costa, D. P. and Faria, C. P. 2008. Conservation priorities for the bryophytes of Rio de Janeiro State, Brazil. *J. Bryol.* 30: 133-142.
- Coxson, D. S. 1991. Nutrient release from epiphytic bryophytes in tropical montane rain forest (Guadeloupe). *Can. J. Bot.* 69: 2122-2129.
- Delgadillo, C. M. 1996. Moss conservation in Mexico. *An. Inst. Biol. Univ. Nac. Auton. Mexico* 67: 177-181.
- Durán, A. D., Cisneros, A. E., and Vargas, V. A. 1992. Evaluación briológica de los efectos de la contaminación atmosférica en la Ciudad de México. [Bryological evaluation of the effects of air pollution in Mexico City.]. *Trop. Bryol.* 6: 71-82.
- Escorcia Ariza, S. C. 1998. Estimados del deterioro de la flora briológica en localidades industrializadas del área metropolitana de San Juan, Puerto Rico. [Estimates of the deterioration of the bryological flora in industrialized localities of the metropolitan area of San Juan, Puerto Rico.]. M. Sc. thesis, University of Puerto Rico, Mayaguez, 93 pp.
- Faus-Kessler, T., Dietl, C., Tritschler, J., and Peichl, L. 2001. Correlation patterns of metals in the epiphytic moss *Hypnum cupressiforme* in Bavaria. *Atmos. Environ.* 35: 427-439.
- Frahm, J.-P. and Gradstein, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *J. Biogeogr.* 18: 669-678.
- Gradstein, S. R. 1992a. Threatened bryophytes of the Neotropical rainforest: A status report. *Trop. Bryol.* 6: 83-94.
- Gradstein, S. R. 1992b. The vanishing tropical rain forest as an environment for bryophytes and lichens. In: Bates, J. W. and Farmer, A. M. (eds.). *Bryophytes and Lichens in a Changing Environment*. Clarendon Press, Oxford, pp. 234-258.
- Gradstein, S. R. 1999. On the rediscovery of *Spruceanthus theobromae* (Lejeuneaceae, Hepaticae), an endangered species on cacao trees in western Ecuador. *Bryobrothera* 5: 81-86.
- Gradstein, R. 2002. Research news from the University of Göttingen. *Bryol. Times* 106: 6-8.
- Gradstein, S. R. 2008. Epiphytes of tropical montane forests-impact of deforestation and climate change. Göttingen Centre for Biodiversity and Ecology. *Biodiv. Ecol. Ser.* 2: 51-65.
- Gradstein, S. R. and Lücking, R. 1997. Synthesis of the symposium and priorities for future research. *Abstr. Bot.* 21: 207-214.
- Gradstein, S. R. and Pócs, T. 1989. Bryophytes. In: Lieth, H. and Werger M. J. A. (eds.). *Ecosystems of the World*. 14B. *Tropical Rain Forest Ecosystems*. Biogeographical and Ecological Studies. Elsevier, Amsterdam, pp. 311-325.
- Gradstein, S. R. and Sporn, S. G. 2010. Land-use change and epiphytic bryophyte diversity in the tropics. *Cambio en el*

- uso de la tierra y diversidad de briófitas epífitas en los trópicos. *Nova Hedw.* 138: 311-323.
- Gradstein, S. R. and Vána, J. 1987. On the occurrence of Laurasian liverworts in the tropics. *Mem. N. Y. Bot. Gard.* 45: 388-425.
- Griffin, D. III. 1974. Observations on bryophyte community of the Poas Volcano, Costa Rica. *Misc. Bryol. Lichenol.* 6: 174-175.
- Gunnarson, U. and Söderström, L. 2007. Can artificial introductions of diaspore fragments work as a conservation tool for maintaining populations of the rare peatmoss *Sphagnum angermanicum*? *Biol. Conserv.* 135: 450-458.
- Hallingbäck, T. and Hodgetts, N. (compilers). 2000. Mosses, Liverworts, and Hornworts. Status Survey and Conservation Action Plan for Bryophytes. IUCN/SSC Bryophyte Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, x + 106 pp.
- Hallingbäck, T. and Tan, B. 1996. Towards a global action plan for endangered bryophytes. *An. Inst. Biol. Univ. Nac. Auton. Mexico* 67: 213-221.
- Herbert, D. A., Fownes, J. H., and Vitousek, P. M. 1999. Hurricane damage to a Hawaiian forest: Nutrient supply rate affects resistance and resilience. *Ecology* 80: 908-920.
- Hietz-Seifert, U., Hietz, P., and Guevara, S. 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. *Biol. Conserv.* 75: 103-111.
- Holz, I. and Gradstein, R. S. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica – species richness, community composition and ecology. *Plant Ecol.* 178: 89-109.
- Hyvönen, J., Koponen, T., and Norris, D. H. 1987. Human influence on the mossflora of tropical rainforest in Papua New Guinea. *Symp. Biol. Hung.* 35: 621-629.
- Jacobsen, N. H. G. 1978. An investigation into the ecology and productivity of epiphytic mosses. *J. S. Afr. Bot.* 44: 297-312.
- Jácome, J., Gradstein, S. R., and Kessler, M. 2011. Responses of epiphytic bryophyte communities to simulated climate change. In: Tuba, Z., Slack, N. G., and Stark, L. R. (eds.). *Bryophyte Ecology and Climate Change*, Cambridge University Press, New York, pp. 191-207.
- Jayasekera, R. and Rossbach, M. 1996. Background levels of heavy metals in plants of different taxonomic groups from a montane rainforest in Sri Lanka. *Environ. Geochem. Hlth.* 18: 55-62.
- Kautz, T. and Gradstein, S. R. 2001. On the ecology and conservation of *Spruceanthus theobromae* (Lejeuneaceae, Hepaticae) from Western Ecuador. *Bryologist* 104: 607-612.
- Koponen, T. 1992. Endangered bryophytes on a global scale. *Biol. Conserv.* 59: 255-258.
- Kürschner, H. and Parolly, G. 1998. Lebensstrategien stammepiphytischer moose in regenwaldern am andenostabhang und im Amazonas-Tiefland von nord-Peru. [Life strategies of epiphytic bryophyte vegetation in rainforests along the eastern Andean slopes and the Amazon lowlands of northern Peru]. *Nova Hedw.* 67: 1-22.
- Kürschner, H., Frey, W., and Parolly, G. 1999. Patterns and adaptive trends of life forms, life strategies and ecomorphological structures in tropical epiphytic bryophytes – A pantropical synopsis. *Nova Hedw.* 69: 73-99.
- Lisboa, R. C. L. and Borges, A. L. I. 1995. Bryophyte diversity in Belém, Para and its potential as pollution indicator for urban areas. *Bol. Mus. Paraense Emilio Goeldi ser. Bot.* 11: 199-225.
- Liu, W.-Q., Lei, C.-Y., and Dai, X.-H. 2007. Bryophyte communities in the forest of Heishiding Nature Reserve, Guangdong, China. *J. Trop. Subtrop. Bot.* 15: 538-544.
- Lodge, D. J. and McDowell, W. H. 1991. Summary of ecosystem-level effects of Caribbean hurricanes. *Biotropica* 23: 373-378.
- Lodge, D. J., Scatena, F. N., Asbury, C. E., and Sánchez, M. J. 1991. Fine litterfall and related nutrient inputs resulting from Hurricane Hugo in subtropical wet and lower montane rain forests of Puerto Rico. *Biotropica* 23: 336-342.
- Loope, L., Duever, M., Herndon, A., Snyder, J., and Jansen, D. 1994. Hurricane impact on uplands and freshwater swamp forest. *BioScience* 44: 238-246.
- Lowman, M., Devy, S., and Ganesh, T. (eds.). 2013. *Treetops at Risk*. Springer, NY, 444 pp.
- Malombe, I., Matheka, K. W., Pócs, T., and Patiño, J. 2016. The ecological response of epiphyllous bryophytes to human-induced edges in Afromontane fragmented forests. *J. Bryol.* 38: 33-46.
- Motito, A. M., Potrony, E., and Reyes, M. D. 1992. Estado actual y perspectivas futuras del estudio de los musgos cubanos. [Current status and future perspectives of the study of Cuban mosses.]. *Trop. Bryol.* 6: 157-160.
- Nadkarni, N. M. 2000. Colonization of stripped branch surfaces by epiphytes in a lower montane cloud forest, Monteverde, Costa Rica. *Biotropica* 32: 358-363.
- Nepstad, D. C., Stickler, C. M., Soares-Filho, B., and Merry, F. 2008. Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point. *Philosoph. Trans. Royal Soc. London B Biol. Sci.* 363: 1737-1746.
- Norris, D. H. 1990. Bryophytes in perennially moist forests of Papua New Guinea: Ecological orientation and predictions of disturbance effects. *Bot. J. Linn. Soc.* 104: 281-291.
- Nöske, N., Hilt, N., Werner, F. A., Brehm, G., Fiedler, K., Sipman, H. J., and Gradstein, S. R. 2008. Disturbance effects on diversity of epiphytes and moths in a montane forest of Ecuador. *Basic Appl. Ecol.* 9: 4-12.
- Odum, H. T., Briscoe, G. A., and Briscoes, C. B. 1970. Fallout radioactivity of epiphytes. In: Odum, H. T. (ed.). *A Tropical Rainforest: A Study of Irradiation and Ecology at El Verde, Puerto Rico*. Atomic Energy Commission, Washington, D.C.
- Olarinmoye, S. O. 1986. Aspects of survival strategies in three common mosses in Ibadan, Nigeria. *Cryptog. Bryol. Lichenol.* 7: 213-218.
- Orrego, O. 2005. Ecological indexes and mathematical models as tools for evaluating the epiphytic bryophyte diversity in Colombian forest patches in the Departamento del Quindío. *J. Hattori Bot. Lab.* 97: 271-280.
- Pardow, A., Gehrig-Downie, C., Gradstein, R., and Lakatos, M. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: Using bryophyte life-forms to detect areas of high biodiversity. *Biodiv. Conserv.* 21: 3637-3655.
- Peck, J. E. 2006. Regrowth of understory epiphytic bryophytes 10 years after simulated commercial moss harvest. *Can. J. Forest Res.* 36: 1749-1757.
- Peck, J. E. and Moyle Studlar, S. 2008. Establishing international guidelines for the sustainable harvest of forest moss. *Evansia* 25: 65-71.
- Peralta, M. G. and Wolf, J. H. 2001. Commercial bryophyte harvesting in the monarch butterfly biosphere reserve, Sierra Chincua, Michoacan, Mexico. *Bryologist* 104: 517-521.

- Petit, E. and Symons, F. 1974. Les bryophytes des bois artificiels de *Cupressus* et d'*Acacia* au Burundi. Analyse factorielle de la végétation bryophytique. [The bryophytes of artificial woods of *Cupressus* and *Acacia* in Burundi. Factor analysis of bryophytic vegetation.]. Bull. Jard. Bot. Nat. Belg. 44: 219-247.
- Pharo, E. J. and Zartman, C. E. 2007. Bryophytes in a changing landscape: The hierarchical effects of habitat fragmentation on ecological and evolutionary processes. Biol. Conserv. 135: 315-325.
- Pócs, T. 1989. A preliminary study of the undergrowth of primary and secondary submontane rainforests in the East Usambara Mountains, with notes on epiphytes. In: Hailton, A. C. and Bensted-Smith, R. (eds.). Forest Conservation in the East Usambara Mountains, Tanzania. The IUCN Tropical Forest Programme, Gland, Switzerland and Cambridge, UK, 392 pp.
- Pócs, T. 1996. Epiphyllous liverwort diversity at worldwide level and its threat and conservation. An. Inst. Biol. Univ. Nac. Auto. Mexico, Ser. Bot. 67: 109-127.
- Pócs, T. 1997. New or little known epiphyllous liverworts, VI. *Papillolejeunea* gen. nov. from Papua New Guinea. Trop. Bryol. 13: 1-18.
- Pócs, T. and Tóthmérész, B. 1997. Foliicolous bryophyte diversity in tropical rainforests. Abstr. Bot. 21: 135-144.
- Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. (ed.). Bryophyte Ecology, Chapman and Hall, London, pp. 333-382.
- Ramovs, B. V. and Roberts, M. R. 2005. Response of plant functional groups within plantations and naturally regenerated forests in southern New Brunswick, Canada. Can. J. Forest Res. 35: 1261-1276.
- Rebello, C. F., Struittaldi-De Vuono, Y., and Domingos, M. 1995. Estudio ecológico de comunidades de briófitas epífitas da Reserva Biológica de Paranapiacaba, SP, em trechos de floresta sujeitos à influência da poluição aérea. [Ecological study of epiphytic bryophyte communities of the Biological Reserve of Paranapiacaba, SP, in stretches of forest subject to the influence of air pollution.]. Revis. Brasil. Bot. 18: 1-15.
- Romero, C. 1999. Reduced-impact logging effects on commercial non-vascular pendant epiphyte biomass in a tropical montane forest in Costa Rica. Forest Ecol. Mgmt. 118: 117-125.
- Sastre de Jesus, I. and Tan, B. C. 1995. Problems of bryophyte conservation in the tropics: A discussion with case examples from Puerto Rico and the Phillipines. Caribb. J. Sci. 32: 200-206.
- Scatena, F. N., Bruijnzeel, L. A., Bubb, P., and Das, S. 2010. Setting the stage. In: Bruijnzeel, L. A., Scatena, F. N., and Hamilton, L. S. Tropical montane cloud forests. Science for Conservation and Management. Cambridge University Press, pp. 3-13.
- Schäfer-Verwimp, A. 1999. Some additions to the bryophyte flora of Dominica, West Indies. Haussknechtia Beih. 9: 317-331.
- Schultze-Motel, W. 1982. The crisis in tropical bryology – a summary. In: Geissler, P. and Green, S. W. (eds.). Bryophyte Taxonomy; Methods, Practices, and Floristic Exploration. Proceedings of the International Association of Bryologists Taxonomic Workshop Meeting, Geneva, pp 505-506.
- Serrano, Y. 1996. The mosses of disturbed areas in the municipality of Bayamon, Puerto Rico. Bryologist 99: 81-84.
- Shi, X.-M., Song, L., Liu, W.-Y., Lu, H.-Z., Qi, J.-H., Li, S., Chen, X., Wu, J.-F., Liu, S., and Wu, C.-S. 2017. Epiphytic bryophytes as bio-indicators of atmospheric nitrogen deposition in a subtropical montane cloud forest: Response patterns, mechanism, and critical load. Environ. Pollut. 229: 932-941.
- Sillett, S. C., Gradstein, S. R., and Griffin, D. III. 1995. Bryophyte diversity of *Ficus* tree crowns from cloud forest and pasture in Costa Rica. Bryologist 98: 251-260.
- Silva, M. P. P. and Pôrto, K. C. 2009. Effect of fragmentation on the community structure of epixylic bryophytes in Atlantic Forest remnants in the northeast of Brazil. Biodiv. Conserv. 18: 317-337.
- Smith, C. W. 1981. Bryophytes and lichens of the Puhima Geothermal Area, Hawaii Volcanoes National Park. Bryologist 84: 457-466.
- Snäll, T., Ribeiro, P. J., and Rydin, H. 2003. Spatial occurrence and colonizations in patch-tracking metapopulations: Local conditions versus dispersal. Oikos 103: 566-578.
- Söderström, L., Hallinbäck, T., Gustafsson, L., Cronberg, N., and Hedenäs, L. 1992. Bryophyte conservation for the future. Biol. Conserv. 59: 265-270.
- Sporn, S. G., Bos, M. M., Hoffstätter-Müncheberg, M., Kessler, M., and Gradstein, S. R. 2009. Microclimate determines community composition but not richness of epiphytic understory bryophytes of rainforest and cacao agroforests in Indonesia. Funct. Plant Biol. 36: 171-179.
- Steege, H. ter and Cornelissen, J. H. C. 1988. Distribution and ecology of vascular epiphytes in lowland rain forest of Guyana. Biotropica 21: 331-339.
- Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M. M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S. R., Guhardja, E., Harteveld, M., Hertel, D., Höhn, P., Kappas, M., Köhler, S., Leuschner, C., Maertens, M., Marggraf, R., Migge-Kleian, S., Moge, J., Pitopang, R., Schaefer, M., Schwarze, S., Sporn, S. G., Steingrebe, A., Tjitrosoedirdjo, S. S., Tjitrosoemito, S., Twele, A., Weber, R., Wolftmann, L., Zeller, M., and Tschamtkke, T. 2007. Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proc. Natl. Acad. Sci. 104: 4973-4978.
- Streimann, H. 1994. Conservation status of bryophytes in Eastern Australia. Trop. Bryol. 9: 117-122.
- Tremblay, R. L. 2008. Ecological correlates and short-term effects of relocation of a rare epiphytic orchid after Hurricane Georges. Endang. Spec. Res. 5: 83-90.
- Turner, I. M., Tan, H. T. W., Wee, Y. C., Ibrahim, A. B., Chew, P. T., and Corlett, R. T. 1994. A study of plant species extinction in Singapore: Lessons for the conservation of tropical biodiversity. Conserv. Biol. 8: 705-712.
- Vareschi, V. 1953. La influencia de los bosques y parques sobre el aire de la ciudad de Caracas. [The influence of forests and parks on the air of the city of Caracas.]. Acta Cienc. Venezuel. 4: 89-95.
- Villaseñor, J. L., Delgadillo, C., and Ortiz, E. 2006. Biodiversity hotspots from a multigroup perspective: Mosses and Senecios in the Transmexican volcanic belt. Biodiv. Conserv. 15: 4045-4058.
- Walker, L. R., Zimmerman, J. K., Lodge, D. J., and Guzman-Grajales, S. 1996. An altitudinal comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. J. Ecol. 84: 877-889.
- Weaver, P. L. 1999. Impacts of Hurricane Hugo on the dwarf cloud forest of Puerto Rico's Luquillo Mountains. Caribbean J. Sci. 35: 101-111.

- Weber, W. A. 1985. Effects on cryptogamic vegetation (lichens, mosses and hepatics). In: El Niño en la Islas Galápagos: El evento de 1982-1983. Fundación Charles Darwin para las Islas Galápagos. Quito, Ecuador, pp. 343-361.
- Werner, F. A. and Gradstein, S. R. 2009. Diversity of dry forest epiphytes along a gradient of human disturbance in the tropical Andes. *J. Veg. Sci.* 20: 59-68.
- Wuethrich, B. 1993. Forests in the clouds face stormy future. *Sci. News* 114: 23.
- Yan, X. L., Bao, W. K., Pang, X. Y., Zhang, N. X., and Chen, J. 2013. Regeneration strategies influence ground bryophyte composition and diversity after forest clearcutting. *Ann. Forest Sci.* 70: 845-861.
- Yeaton, R. I. and Gladstone, D. E. 1982. The pattern of colonization of epiphytes on calabash trees (*Crescentia alata* HBK) in Guanacaste Province, Costa Rica. *Biotropica* 14: 137-140.
- Zander, R. H. and During, H. J. 1999. *Neophoenix* (Pottiaceae), a new African moss species found through soil diaspore bank analysis. *Taxon* 48: 657-662.
- Zartman, C. E. 2003. Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. *Ecology* 84: 948-954.
- Zartman, C. E. and Nascimento, H. E. 2006. Are habitat-tracking metacommunities dispersal limited? Inferences from abundance-occupancy patterns of epiphylls in Amazonian forest fragments. *Biol. Conserv.* 127: 46-54.
- Zartman, C. E. and Shaw, A. J. 2006. Metapopulation extinction thresholds in rain forest remnants. *Amer. Nat.* 167: 177-189.
- Zhang, Li. 2001. Diversity and conservation of Hong Kong bryophytes. Ph.D. thesis, The University of Hong Kong. In English. ix + 303 pp.
- Zotz, G. and Bader, M. Y. 2009. Epiphytic plants in a changing world-global: Change effects on vascular and non-vascular epiphytes. *Prog. Bot.* 70: 147-170.